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STUDIES IN THE GENUS DIPLACUS (SCROPHULARIACEAE)

HOWARD E. McMINN

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STUDIES IN THE GENUS DIPLACUS, SCROPHULARIACEAE

Howard E. McMinn

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Introduction

The present study of the genus *Diplacus* was begun in 1944 with two primary objects in view, one to ascertain the probable biological relationships and evolution among the wild entities (taxa, sing. taxon), and the other to discover and to produce more desirable forms for garden ornamentals. I had been interested in the taxonomic aspects of the genus for several years. The amount of probable genetic variation which occurred in the field and in the garden wherever two or more taxa came into contact was impressive. Equally interesting was the lack of variation wherever a taxon was geographically isolated from any other taxon. Mr. Maunsell Van Rensselaer, director of the Santa Barbara Botanic Garden, was interested in the group because of its ornamental potentialities, and he suggested that studies be made of the genus which would include both its taxonomic and ornamental aspects. Because of the opportunity afforded for carrying on studies involving both plant taxonomy and horticulture, a program of investigation was thus undertaken which called for extensive field and herbarium studies, garden culture, and artificial hybridization. The observations, experiments, speculations, and conclusions recorded in this paper represent the work done in the field, in private and public gardens, at various herbaria listed under acknowledgments, and at the William Joseph McInnes Memorial Garden at Mills College, Oakland, California.

The genus *Diplacus,* or the section *Diplacus* of the genus *Mimulus* of some authors, belongs to the Figwort Family, Scrophulariaceae. As treated in this paper the genus consists of fourteen named field entities, which are described as binomials, and numerous unnamed hybrids and their derivatives. The plants, which are usually soft-wooded, sub-shrubby, bushy perennials, are commonly known as Bush or Sticky Monkey-flowers.

Madroño, Vol. 11, No. 1, pp. 1–32. February 13, 1951.

Choice of Names. Since this paper has been written for horticulturists, nurserymen, and plant-minded laymen as well as for botanists, and since complete agreement has not been reached by botanists as to the status of species, subspecies, and varieties, I have chosen to treat all these field entities (taxa) simply as binomials. Inasmuch as binomials to most botanists indicate species, I have endeavored not to use the word species when writing of these various entities. I must point out, however, that if sterility and geographical distribution tests were the main criteria applied in delimiting species and subspecies, then the field entities of the genus *Diplacus* probably would be classified as two taxonomic species, eleven subspecies, and numerous hybrids. (See sections on Hybrids and Probable Biological Relationships and Evolution.)

Acknowledgments. It is with sincere appreciation of the assistance given and the courtesies shown by many individuals during the progress of this study, that I take this opportunity to express my grateful acknowledgments.

I am especially indebted to Mrs. Blanche Rice McInnes who supplied funds for the building of the greenhouse, lathhouse, and for the upkeep of the garden at Mills College where most of the experimental work has been conducted; to Mr. Maunsell Van Rensselaer for suggesting the genus for critical study, for supplying seed of several of the wild forms, and for valuable aid given in many other ways; to Dr. G. Ledyard Stebbins, Jr. for his aid in starting the program of artificial hybridization and his continued interest and encouragement during the entire study; to the following for collecting seed or for supplying living and pressed material: Mr. L. L. Edmunds, Mrs. Hans Ewoldsen, Mr. F. F. Gander, Mrs. Ethel B. Higgins, Mr. J. F. Macbride, Mr. J. H. Munhall, Mr. Clifton Smith, Mr. Edward Stuhl, and Col. John R. White; to Mr. L. A. Snyder for supplying information on the chromosome-numbers of certain entities; to Dr. F. W. Pennell for exchange of ideas on key characters and identity of some type specimens; to Mr. Rex Ramer and Mr. D. H. Sheffield for making arrangements for the chemical analyses of the stems and leaves of *Diplacus aurantiacus* by the Naval Stores Department of the Hercules Powder Company, Wilmington, Delaware; and to Mrs. Helen R. McMinn and Miss Caroline Krogness for assistance in reading of the proof.

For helpful criticisms and reading of parts of the manuscript I am most grateful to Dr. David Keck, Dr. Herbert Mason, Dr. Lincoln Constance, Dr. Jens Clausen, and Dr. W. M. Hiesey. However, I alone must be held responsible for any errors in observation, judgment, speculation, expression, and conclusions.

The granting of a leave of absence during the spring of 1950 by President Lynn T. White, Jr. and the Board of Trustees of

Mills College made it possible for me to visit herbaria in England and to complete most of the writing of the manuscript. For this I am truly grateful.

Financial help from the Santa Barbara Botanic Garden, courtesy of Mr. and Mrs. Harold Chase, the William Joseph McInnes Memorial Garden Fund, and the Zelinsky Foundation made it possible to extend my field and herbarium observations and aided in the preparation of the manuscript and its publication.

The curators of herbaria at the following institutions, designated in the section on Taxonomic Treatment by the initials as here given, have either sent me specimens or permitted me to examine specimens from collections in their care:

BM,	British Museum of Natural History, London.
CA,	California Academy of Sciences, San Francisco, California.
CM,	Carnegie Museum, Pittsburgh, Pennsylvania.
D,	Dudley Herbarium, Stanford University, California.
G,	Gray Herbarium, Harvard University, Massachusetts.
K,	Royal Botanical Gardens, Kew.
MO,	Missouri Botanical Gardens, St. Louis, Missouri.
NY,	New York Botanical Gardens, New York.
P,	Pomona College, Claremont, California.
SD,	San Diego Natural History Museum, San Diego, California.
SM,	Santa Barbara Museum of Natural History, Santa Barbara, California.
UC,	University of California, Berkeley, California.
UC–Cl,	Clokey Herbarium, University of California, Berkeley, California.
UC–J,	Jepson Herbarium, University of California, Berkeley, California.
UC–VTM,	Vegetative Type Map Herbarium, University of California, Berkeley, California.

Photographs for the half-tone illustrations, figures 8, 9, 12–15, 18–23, and 25–27 were taken by Roi Partridge; figures 10 and 24 by the British Museum of Natural History; and figure 16 by Mr. Meidel Applegate. Drawings for figures 5a, b, and 6 were prepared by Miss Marie Pettibone, for figures 3t–z, 5e, f, i, by Mrs. Katherine Uhl Ball, for 3a–s, by Miss Joan Gross, and for figures 5c, d, g, h, by Miss Martha McMaster.

Finally, for the critical reading of the entire manuscript and for suggestions in preparing it for the publisher, I am most grateful to Miss Annetta Carter, Dr. Rimo Bacigalupi, and Dr. Helen Sharsmith.

General Distribution

The fourteen natural entities of the genus *Diplacus* described in the section on Taxonomic Treatment occur only in the western United States and northern Mexico. In this area they are distributed from southwestern Oregon southward in the Coast Ranges to the mountains of southern California and northern Lower California, on the islands off the coast of southern California and Lower California, and on the lower western slopes of the Sierra Nevada from Butte and Plumas counties southward to Tuolumne County and from Fresno County southward to the Tehachapi Mountains (figs. 1, 2).

No two entities have quite the same (sympatric) distribution, but in several areas two or more entities overlap along the borders of their geographical ranges. If these overlapping areas contain disturbed habitats such as fireburns, erosion washes, landslides, road cuts, change in land use, and other natural or man-made upheavals, they most likely will be populated by a complex hybrid swarm formed by the crossing of the invading entities and subsequent backcrossing. Anderson (1948, 1949) refers to these new habitats as "hybridized habitats", and to the complex of intercrossing and backcrossing as "introgressive hybridization", connotations deserving much consideration.

Most of the entities thrive best in rocky soils, commonly of granitic origin, or in soils underlaid by decomposing rock in the lower mountain canyons, road cuts, hillsides, or other areas where rock surfaces are exposed. In most localities they occur as successional plants, associated with the more permanent species of the Northern Coastal Scrub and Closed-cone Pine plant communities of the Oregonian Biotic Province and of the Coastal Sage Scrub, Chaparral, Woodland and Southern Oak Woodland plant communities of the Californian Biotic Province, and occasionally with species of the Yellow Pine Forest community of the Sierra Biotic Province (Munz and Keck, 1949).

In order to get a clear picture of the distribution of the various natural entities, we shall begin in southwestern Oregon, the northern limit of the geographical range for the genus. Here we find *D. aurantiacus* which continues southward in California as far as Santa Clara and Santa Cruz counties with very little variation in morphological characters. In San Benito, Monterey, San Luis Obispo, and northwestern Santa Barbara counties this northern entity often shows the effects of contamination of genes from *D. fasciculatus* and *D. longiflorus*. These forms will be discussed further under the section dealing with natural hybrids.

On the eastern slope of the Pozo Range in central San Luis Obispo County *D. longiflorus* occurs. Continuing in a southeastern swing around the southern end of the "Great Valley" in the Tehachapi Mountains of Kern County to the southern Sierra

Nevada, we find *D. calycinus* in a few scattered localities. As we go northward along the western slope of the Sierra Nevada to Fresno County, almost all plants of *Diplacus* are easily identified as *D. calycinus,* but a few specimens appear to be intermediate between *D. calycinus* and *D. longiflorus,* an entity which has been found north of Bakersfield.

North of Fresno County lie Madera and Mariposa counties where, to my knowledge, no specimens of *Diplacus* have ever been found growing naturally. As we continue northward along the lower Sierra Nevada into northern Tuolumne and extreme eastern Stanislaus counties we again find *D. aurantiacus,* which extends northward through Calaveras, Amador, eastern Sacramento, and Eldorado counties to southwestern Placer County. A slight hiatus in distribution now occurs, but as we enter the drainage basin of the Bear River of Placer and Nevada counties we encounter *D. grandiflorus.* This entity occurs northward in the granite canyon areas of the Yuba and Feather rivers in Sierra, Yuba, Butte, and western Plumas counties. The divide between the North Fork of the American River and the Bear River seems to be a barrier separating *D. aurantiacus* of the central Sierra Nevada from *D. grandiflorus* of the northern Sierra Nevada.

Returning to the South Coast Ranges, in southern San Luis Obispo County and south into Santa Barbara County we find that most specimens can be identified as *D. aurantiacus, D. fasciculatus, D. longiflorus,* or *D. lompocensis,* but several appear to be hybrids involving genes from these four entities. Plants on Lompoc Mesa and adjacent areas appear to constitute an incipient "subspecies", more closely resembling *D. longiflorus* than any other entity. It is here described on p. 62 as a new species.

Thus far in our distributional itinerary we have encountered plants with flowers which are yellow, buff, or orange in varying hues. We meet our first plants with reddish flowers as we approach southeastern Ventura and western Los Angeles counties. Here, associated with *D. longiflorus,* we find a red-flowered *Diplacus* which has been called *D. rutilus* and which probably has been derived as the result of introgressive hybridization involving crosses between the yellow-flowered *D. longiflorus* and the red-flowered *D. puniceus.* These plants resemble *D. longiflorus,* except for color, and are found associated with that entity in several scattered localities in Los Angeles, Orange, and western Riverside counties, and in northern Lower California. Most of the plants tested are homozygous for the red flower color.

In southeastern Los Angeles County, western Riverside County, and in the Santa Ana Mountains of Orange County, plants of *D. longiflorus, D. rutilus, D. puniceus,* and *D. australis* occur. Wherever two or more of these entities overlap in their distribution, many hybrids are found and in some regions these hybrid populations seem to dominate the areas to the near exclusion of

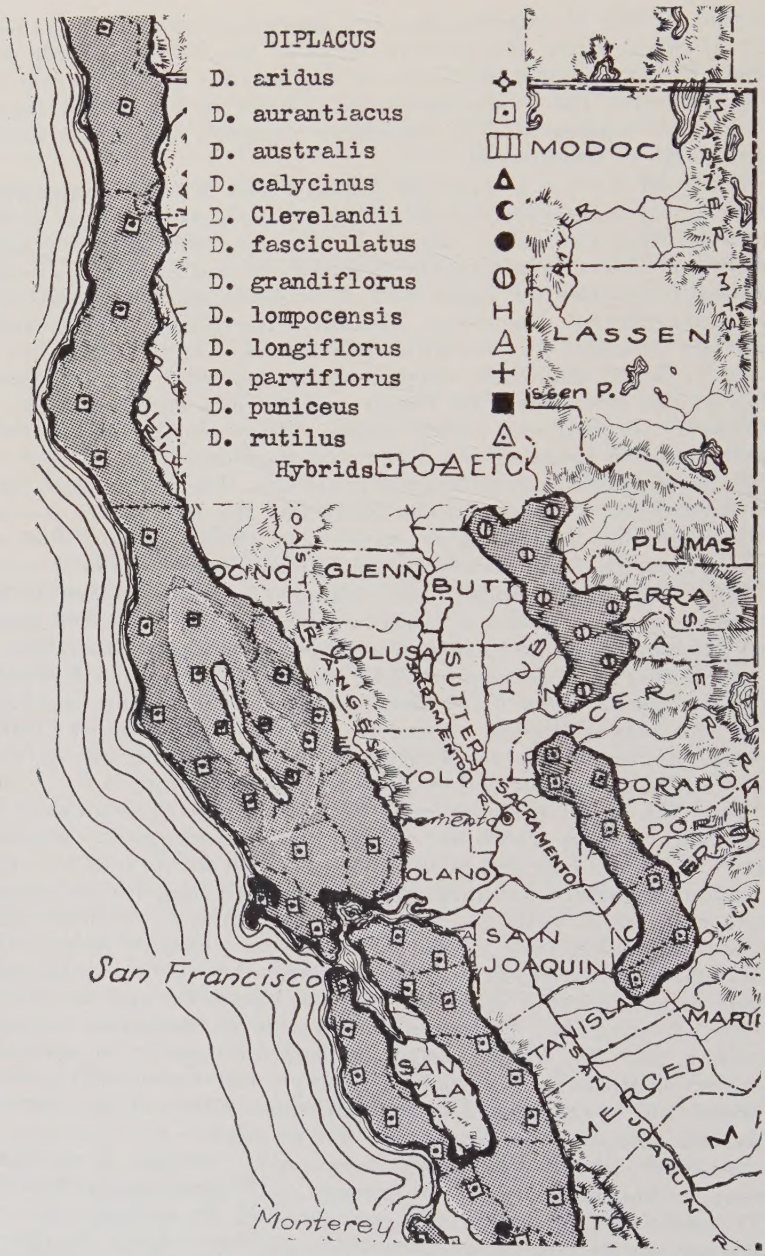


Fig. 1. Distribution of *Diplacus* in northern California and southern Oregon.

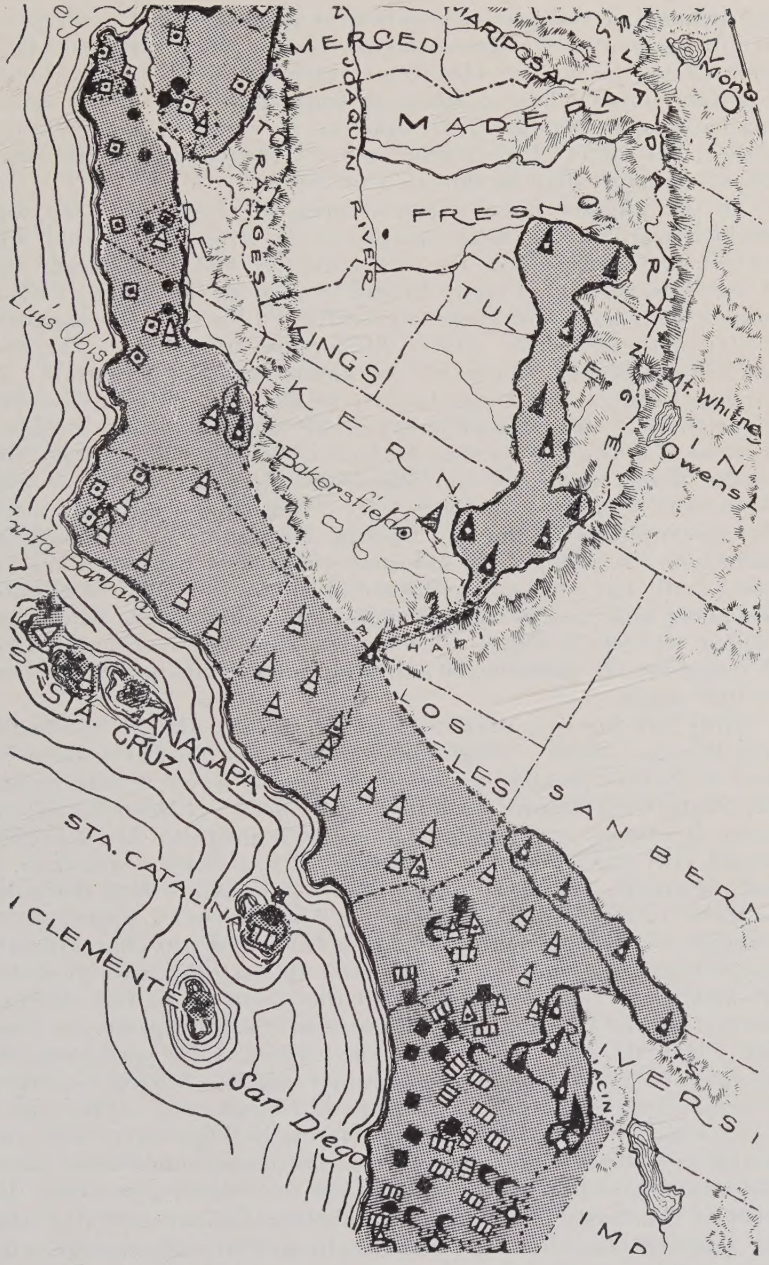


FIG. 2. Distribution of *Diplacus* in southern California, Lower California, and the coastal islands.

one or more of the probable ancestral parents. In the Trabuco area of the Santa Ana Mountains, *D. Clevelandii,* a species usually confined to the higher elevations, extends down to the lower mountain slopes where it comes in contact with the lower elevation entities, *D. longiflorus, D. puniceus, D. australis,* and their hybrids. The effect of gene flow from *D. Clevelandii* into *D. longiflorus* is quite evident in this area of contact.

In the Laguna Beach Canyon area of Orange County and southeastward into extreme southwestern Riverside County and central and western San Diego County we find *D. puniceus* and *D. australis,* as well as many hybrid swarms in the areas of overlapping distribution of these two entities. No true *D. longiflorus* occurs in these areas. At the higher elevations of the central San Diego County mountains we again find *D. Clevelandii.* In northeast central San Diego County we find the southernmost distribution of *D. calycinus,* an entity occurring in scattered localities northward in the San Jacinto Mountains of Riverside County and on the desert slopes of the San Bernardino Mountains in San Bernardino County. In times past it probably continued along the desert slopes of the San Gabriel Mountains of Los Angeles County to the Tehachapi Mountains of Kern County where it could easily have spread northward in the southern Sierra Nevada and in the inner South Coast Ranges. In southeastern San Diego County we find *D. aridus.* In northern Lower California, Mexico, *D. longiflorus, D. puniceus, D. australis,* and hybrids involving these entities occur.

Still left for consideration are the islands off the California and Mexican coasts. Beginning at the north on Santa Rosa Island we find *D. parviflorus, D. longiflorus,* and a few hybrid plants. On Santa Cruz Island we find *D. parviflorus, D. longiflorus,* and many specimens of hybrids of these two entities. On Anacapa Island only *D. parviflorus* is known. Continuing southward to Santa Catalina Island we find that most plants are with difficulty assigned to any definite "species." They appear to represent a complex of forms probably resulting from past crossing and subsequent backcrossing of *D. puniceus, D. australis,* and probably *D. longiflorus.* At present most of the plants show the effect of genes from *D. puniceus* and *D. australis.* A few specimens from San Clemente Island have been identified as *D. parviflorus,* although one specimen (*Nell Murbarger 33,* UC 557829) appears intermediate between *D. parviflorus* and *D. puniceus.* A few specimens which were named *D. stellatus* by Kellogg have been collected on Cedros Island, Mexico, but until more and better material can be secured it is not possible to evaluate properly this entity. At least three collectors visiting Cedros Island during the past ten years have been unable to find any *Diplacus* growing there. This entity may have become extinct due to drought and over-browsing by goats.

Representative localities and specimens for these natural entities are cited in the section on Taxonomic Treatment.

General Morphology

Roots. The root system of *Diplacus* varies with the conditions under which the plants grow. In granite clefts and on rocky bluffs an extensive taproot develops, while lateral roots, growing in available dirt-filled crevices, may spread from two to four feet to reach a source of water. Where the soil is rocky, but contains more water-holding humus, the taproot is usually short and the lateral root system is not so deep. The roots do not seem able to penetrate deeply into heavy soils, and when grown in rather heavy garden soils, the plants develop a shallow, weak root system.

Stems. The stems, which are always perennial and woody, at least at or near the ground, vary from 1 to 8 feet in height. The plants may be freely branched from the base or more erect with fewer lateral branches. The bark on older stems cracks and peels off in thin papery flakes. On the younger stems the bark is smooth, usually somewhat glutinous, glabrous or hairy, and green, yellow, or pale red in color.

Leaves. The leaves are simple, opposite, evergreen, and sessile, or rarely short-petioled, those of the upper branches often bearing in their axils short, lateral branchlets with several smaller leaves. The blades are ½ to 4 inches long and vary in outline from linear, to lanceolate, elliptic, or ovate. The upper surface is glandular, glabrous or microscopically puberulent, and often impressed-veiny, the lower surface glandular, glabrous or microscopically puberulent to densely villous. The margins are entire or toothed and often revolute.

A study of the internal anatomy of the leaf shows it to be of the mesophytic type in spite of the dry habitats in which the plants usually grow. The leaves are bifacial and vary in thickness from 100 to 253μ. They are composed of an upper cuticle layer 2.7 to 9.5μ thick; upper epidermis 5.4 to 19μ thick; palisade tissue of two to six layers of cells composing about one-half of the mesophyll, the individual cells from 12 to 33μ long; an irregularly loosely arranged mass of spongy cells composing nearly one-half of the mesophyll, the individual cells 9.4 to 19.6μ in diameter; lower epidermis 2.7 to 10μ; and the lower cuticle layer from negligible to 2.6μ. Sessile and stalked multicellular glands usually occur on both surfaces. The trichomes (fig. 3, a–s) vary from single and simple to branched and multicellular, and from few and scattered on the upper surface to numerous and densely matted on the lower surface. Ten measurements, from leaves embedded in paraffin and sectioned, were made for each of the seven characters listed above upon *D. aridus, D. auran-*

tiacus, D. grandiflorus, D. calycinus, D. longiflorus, and *D. puniceus.*

The exudation from the leaf-glands of *D. aurantiacus,* according to Sheffield (1949), is in the nature of a resin, similar in some

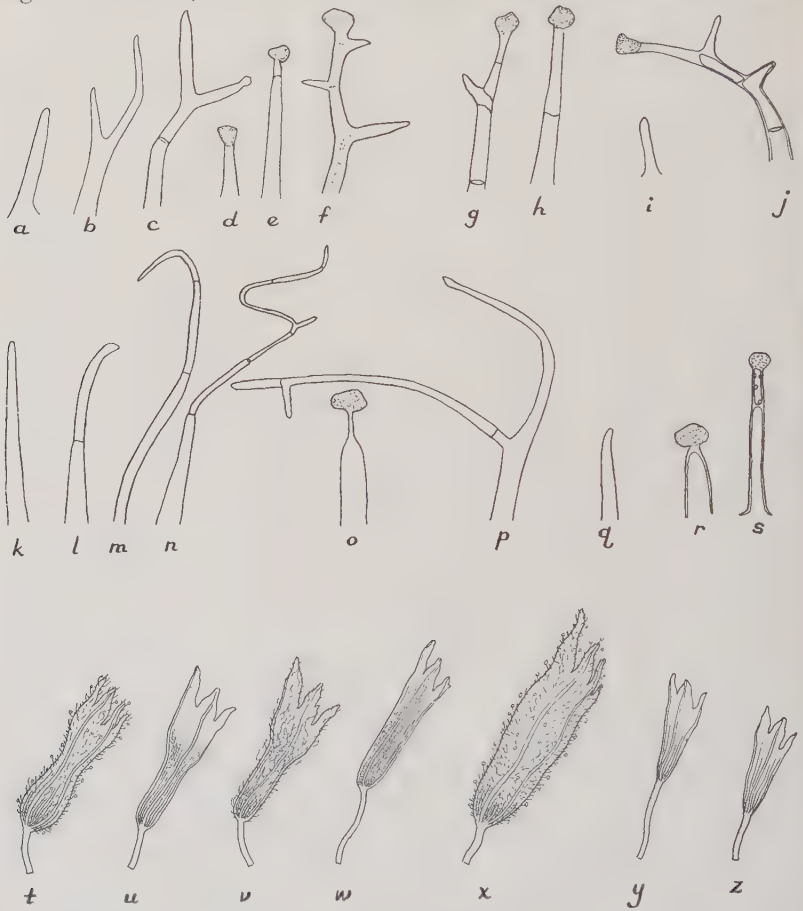


Fig. 3. Variation in trichomes and calyces in *Diplacus.* Trichomes, *a–s: a–f,* from leaves; *g–j,* from upper branchlets; *k–p,* from calyces; *q–s,* from pedicels. Calyces, *t–z: t, D. Clevelandii,* glandular-hairy with bulbous base; *u, D. aridus,* glabrous, with flared throat; *v, D. calycinus,* hairy, with flared throat; *w, D. puniceus,* glabrous and trim; *x, D. longiflorus,* glandular-hairy and swollen; *y* and *z, D. aurantiacus,* glabrous and expanding upward, small type found in some plants. (Approximately natural size.)

respects to the exudation from the Creosote Bush, *Larrea divaricata,* of the desert regions of the arid Southwest.

Flowers. The flowers are borne singly in the axils of the upper leaves. The pedicels vary from 1/8 to 1 inch in length and are glabrous to glandular-puberulent. The calyces (fig. 3, t–z),

which are tubular-prismatic in outline, 3/4 to 1 1/2 inches long, and glabrous to glandular-hairy, usually have a narrow tube which gradually or abruptly expands into a swollen to flared throat terminated by five unequal short teeth. The funnelform corollas (fig. 4) are 1 1/4 to 2 1/2 inches long, and of varying shades of

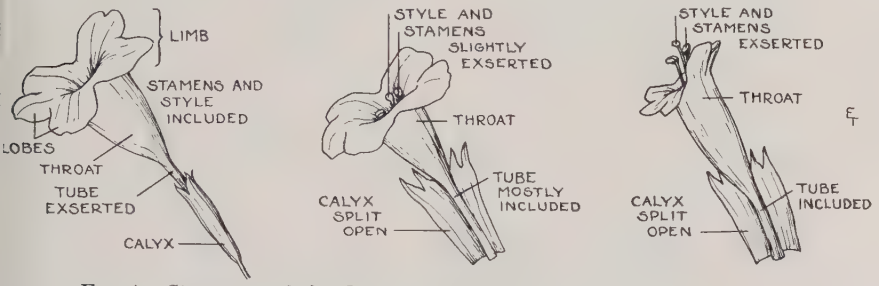


Fig. 4. Structure of the flowers of *Diplacus*.

yellow, orange, buff, and red. They are differentiated into a distinct tube, throat, and limb. The tube is narrowly cylindrical, 1/2 to 1 3/8 inches long, included within or exserted from the calyx, and expands into a narrow funnelform or bell-shaped throat 1/2 to 1 inch long bearing two yellow, longitudinal bands. The bilabiate limb (fig. 5i) has a dorso-ventral spread of 3/4 to 2 inches, and the two upper lobes, which usually extend at right angles from the throat but may be recurved or extended slightly forward, commonly have a pronounced lateral notch and a few to several secondary serrations, or they may be nearly entire. The three lower lobes have a lateral spread of 5/8 to 1 3/4 inches and usually extend forward from the throat, but may be rotate or slightly recurved. They commonly have small serrations at their tips, but may be shallowly to deeply bifid or rarely entire. The stamens (fig. 5d) are four, in two pairs of unequal length; the two shorter are attached to the lower side of the tube near its junction with the throat and the two longer are attached to the upper side of the tube at about the same level. The filaments are typically glabrous and often glandular. The anthers of each pair are connivent and either included or exserted from the throat of the corolla. The single pistil (fig. 5d) has a small, glabrous ovary and a slim, glabrous to glandular-puberulent style terminated by two equal or subequal glandular-hairy, broadened stigma-lobes (figs. 5e, f) which close when irritated mechanically or with pollen. At anthesis, the open stigma extends above the anthers and thus facilitates cross pollination by insects and humming birds. The pollen (figs. 5a, 6a–h) when dry is broadly elliptical, averaging 48μ long and 32μ wide, and has five (4 to 7) longitudinal furrows extending nearly to the rounded ends. The surface is finely roughened or pitted as in an orange, or slightly reticulate. When moist the pollen is broadly oval to nearly

spherical. In all field entities, with the exception of *D. Clevelandii,* the pollen is usually 90 to 100 per cent fertile. In the few flowers of *D. Clevelandii* examined the pollen varied from 33 to 70 per cent in fertility. The ovary (fig. 5c) is composed of two carpels with parietal placentation, the placentae meeting but not uniting in the center.

Fruit. The fruit (fig. 5h) is a firm, linear to ovate-oblong, somewhat cylindrical, two-valved capsule 3/8 to 1 inch long, and is enclosed in the dried calyx. It usually splits down the upper suture, thereby exposing the flat surfaces of the two thin, papery extensions of the flange-shaped placentae attached to the two valves. The open fruit appears somewhat boat-shaped. In *D. Clevelandii* the capsule (fig. 5g) when mature splits from the tip along four lines.

Seeds. The numerous, small seeds (figs. 5b, 6c, d) averaging about 1 mm. in length are broadly oval, tapering to either end, and have finely roughened and reticulated surfaces. When the capsules are open the seeds are hidden beneath the flanges of the placentae.

Chemical Nature of the Benzene Extract from Stems and Leaves of Diplacus aurantiacus

A sample of stems and leaves of *Diplacus aurantiacus* was examined by the Research Department Experiment Station of the Hercules Powder Company, Wilmington, Delaware, and the results communicated to me by Mr. O. H. Sheffield (1949). The following analysis was reported for a 9.14 per cent yield of a dark friable resinous residue obtained after removing the benzene and liquid extract from the resin present:

Acid number 57
Drop softening point ..... 87, 88°C.
Ultraviolet observations:

1. Similar to a fraction of the neutral bodies in resin
2. No abietic structure present
3. Has phenolic nature
4. Flavonic-type structure

"Only a trace of liquid extract was isolated by fractional distillation of the benzene. Both the resinous and the liquid extract had an odor very similar to that of dry alfalfa.

"The resin in some respects seems similar to Creosote Bush

Explanation of the Figures. Figure 5.

Fig. 5. Floral morphology: *a,* pollen grain, × 375; *b,* seed, × 25; *c,* cross-section of mature ovary showing two carpels and parietal placentae, × 10; *d,* longitudinal section of corolla showing stamens in two pairs of unequal length, and single pistil with bilobed stigma, × 1½; *e,* stigmatic lobes appressed, × 2; *f,* stigmatic lobes open, × 2; *g,* mature fruit of *D. Clevelandii,* with four lines of dehiscence from the apex, × 2; *h,* mature fruit typical of other species than *D. Clevelandii,* × 2; *i,* corolla lobes showing variation in size and configuration, × 1.

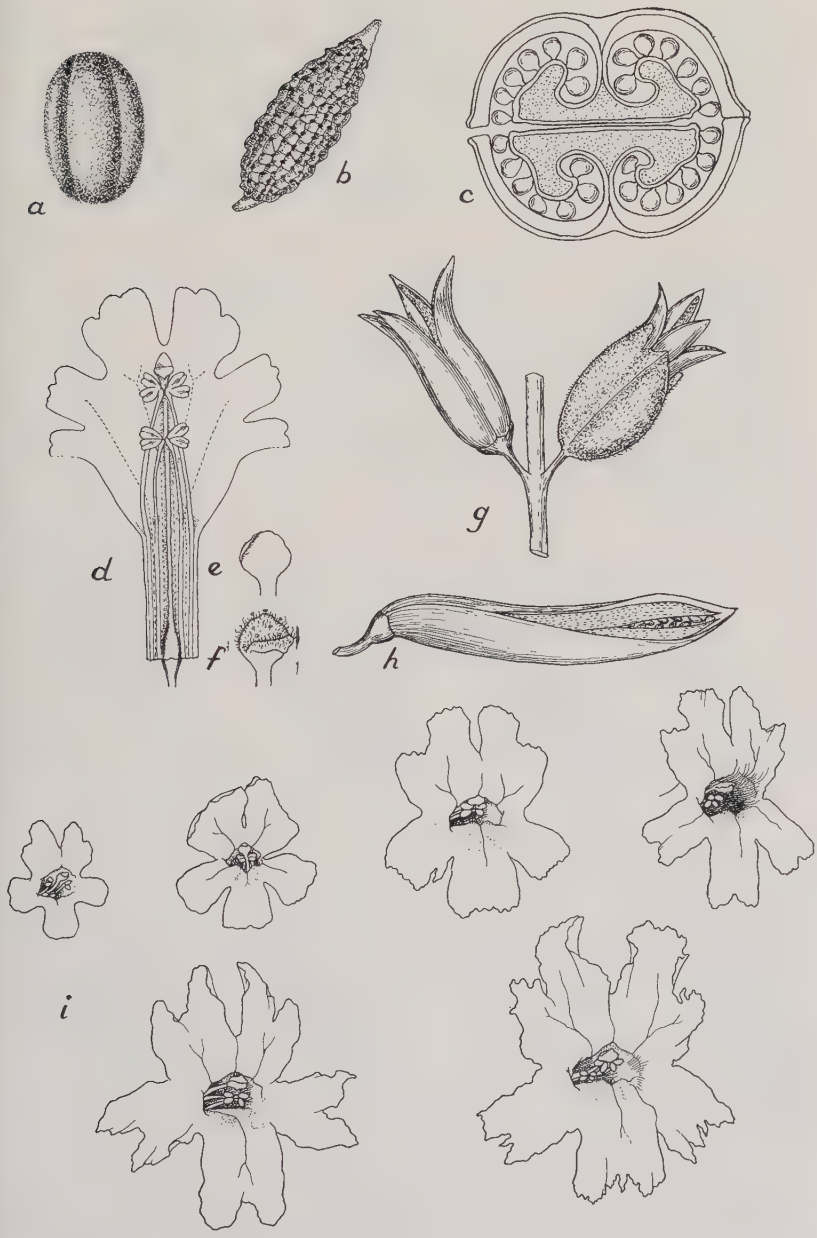


FIG. 5. Floral morphology.

Fig. 6. Pollen and seeds in *Diplacus*. Dry pollen, × 450, *a–e*: *a*, *D. fasciculatus*; *b*, *D. aridus*; *c*, *D. Clevelandii*; *d*, *D. puniceus*; *e*, *D. Clevelandii*, sterile grain. Fresh pollen of *D. longiflorus*, × 600, *f–h*: *f*, lateral view; *g*, polar view; *h*, median optical view. Seeds, × 30, *i–p*: *i*, *D. grandiflorus*; *j*, *D. longiflorus*; *k*, *D. parviflorus*; *l*, *D. australis*; *m*, *D. Clevelandii*; *n*, *D. aurantiacus*; *o*, *D. puniceus*; *p*, *D. aridus*.

Resin. Suggested uses for this resin included varnishes, insulating compounds, adhesives, sizes and rubber compounding."

Cytology

Cytological investigations on *Diplacus* were carried on by Dr. G. Ledyard Stebbins, Jr. and Mr. Leon Snyder at the College of Agriculture, Division of Genetics, University of California, Berkeley, California. The cytology of the pollen mother cells of five species and one hybrid was investigated for their chromosome numbers. From material obtained from living plants in the garden of Dr. H. L. Mason in Berkeley, Stebbins reported the diploid number for both *D. calycinus* and *D. puniceus* to be (2n =) 20. Likewise, that of *D. fasciculatus,* based on material obtained from living plants growing in the wild state on the Francis Simes Hastings Natural History Reservation in northern Monterey County, is presumed to be (2n =) 20, since Stebbins reported the haploid number as (n =) 10. Snyder further reported n = 10 for *D. Clevelandii* (Santa Ana Mts., McMinn Lot 2–2), n = 10 for *D. aridus* (Jacumba, McMinn Lot 4), and n = 10 for *D. longiflorus* × *D. Clevelandii* (Santa Ana Mts., McMinn Lot 17) (fig. 7).

According to Snyder (1949), the material was fixed in a 3 to 1 mixture of absolute alcohol and glacial acetic acid respectively for twenty-four hours and then stored in 70 per cent alcohol. It was subsequently smeared in propionic carmine, after acetocarmine was tried with no great success. With propionic carmine, the chromosomes were distinctly differentiated from the surrounding cytoplasm, since this reagent does not stain the cytoplasm so deeply as does acetocarmine. The slides containing smears of *D. aridus* and *D. Clevelandii* were subsequently destained with acetic acid to lighten the cytoplasm even more.

From these investigations, it appears that all meiotic divisions are regular and that n = 10 is probably the haploid number for all the entities of this relatively small genus. This number and the regularity in the behavior of the chromosomes during meiosis seem to indicate that any cytological barriers to the successful crossing of the field entities must be in the nature of gene incompatibilities. Such barriers must be of only slight consequence, for, as will be later shown, artificial hybrids involving nearly all of the field entities have been easily and successfully produced.

Taxonomic Treatment

Diplacus Nutt. Taylor's Ann. Nat. Hist. Ser. 1, no. 1: 137 (1838). Name proposed October 12, 1837.

Mimulus section *Diplacus.* Gray, Proc. Am. Acad. 11: 97 (1876); Bot. Calif. 1: 565 (1876).

Nearly evergreen subshrubs or shrubs, 1 to 3 or rarely 8 feet tall, with branches erect or spreading from near the base and with glandular and glabrous, viscid-pubescent, or villous herbage.

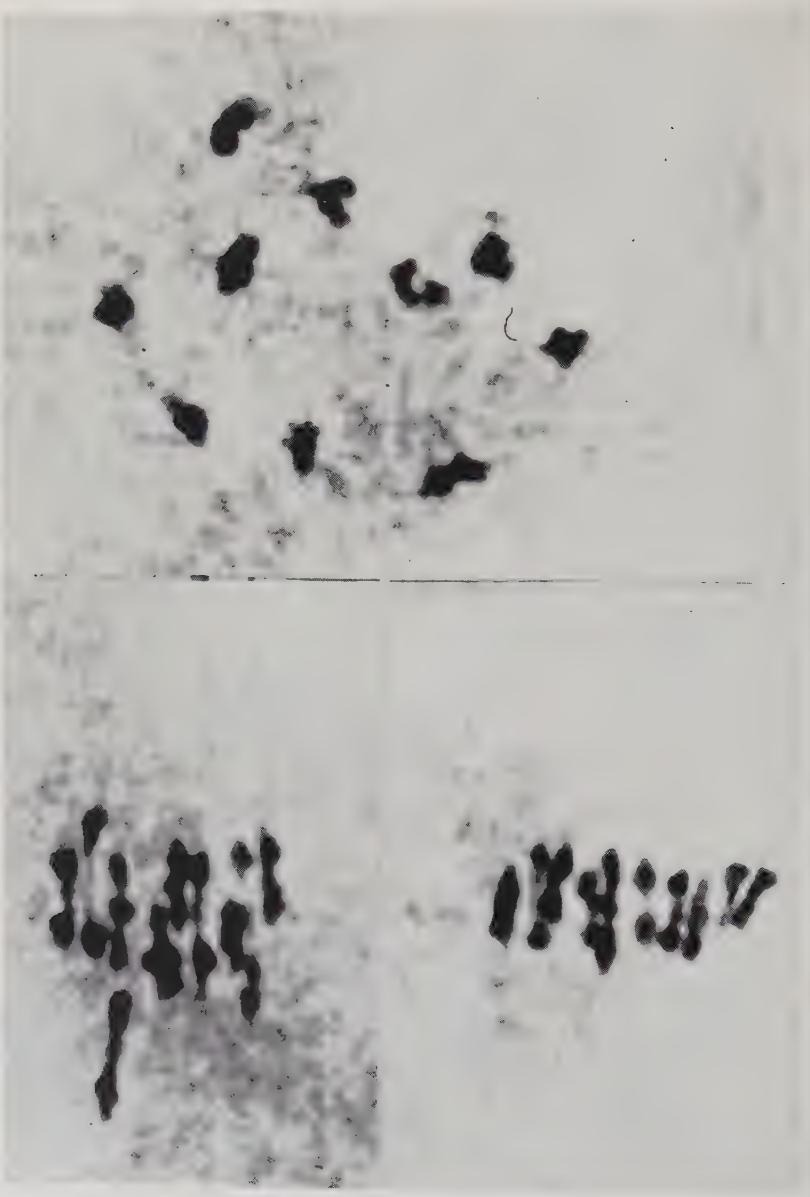


FIG. 7. Photomicrographs of chromosomes from temporary smears prepared by Leon Snyder, × 3390: *a*, diakineses, *D. Clevelandii; b*, first metaphase, *D. longiflorus* × *D. Clevelandii*, Lot 17; *c*, first metaphase, *D. aridus*.

Leaves simple, opposite, sessile or rarely short-petioled, often apparently clustered on short lateral branchlets borne in the axils of the upper stem-leaves; blades linear, lanceolate, elliptic, oblong-lanceolate, or ovate; margins entire or toothed and often revolute. Flowers bisexual, irregular, borne singly in the axils of the upper leaves; pedicels 1/8 to 1 inch long; sepals 5, joined into a narrow tube which gradually or abruptly expands into a throat terminated by 5 unequal short teeth; corolla of varying shades of yellow, orange, buff, and red, 5-lobed, the funnelform tube expanding above into a throat and bilabiate limb; stamens 4, distinct, in 2 pairs of unequal length, attached to the corolla-tube; pistil 1, with 2 carpels, the ovary superior and with parietal placentae. Fruit a linear or oblong-cylindrical, 2-valved capsule. Seeds small, numerous, broadly oval, with finely roughened and reticulated surfaces.

Artificial Key to the Field Entities

I. Plant nearly herbaceous, woody only at base; leaves finely glandular-pubescent on both surfaces; calyces usually swollen at base; corollas deep lemon-yellow, the tube not exserted beyond the calyx-throat, the lobes about equal and nearly entire; capsules 3/8 to 1/2 inch long, splitting at the apex into 4 sharp-pointed divisions; Santa Ana Mountains and the high mountains of San Diego County ..... 1. *D. Clevelandii*, p. 51

II. Plants distinctly woody at and above the base, often distinctly shrubby; leaves not glandular-pubescent above, glabrous or more or less glandular and pubescent beneath; calyces not swollen at base; capsules 1/2 to 1 inch long, splitting along the upper suture and thus becoming boat-shaped when mature.

A. Corollas orange, copper, yellow, buff, cream-colored, or nearly white, never truly red.

1. Calyces, lower leaf-surfaces, and upper branchlets glabrous or microscopically to barely visibly glandular-puberulent.

a. Leaves slightly to distinctly impressed-veiny above; corolla-tube typically not exserted beyond the calyx-throat.

Corollas deep orange to yellow-orange.

Corollas 3/4 to 1 1/8 inches broad; leaves distinctly impressed-veiny above; calyces, pedicels, and lower surface of upper leaves often with a close coat of minute hairs;

North and South Coast Ranges and lower, middle altitudes of the central Sierra Nevada ..... 2. *D. aurantiacus*, p. 54

Corollas less than ¾ inch broad; Cedros Island ..... 13. *D. stellatus*, p. 84

Corollas light orange, orange-yellow, cream-colored to nearly buff, the inner side of throat typically buff or nearly white, 1⅛ to 1½ inches broad; leaves only slightly impressed-veiny above.

Calyces slender, scarcely broadening upward; calyces, pedicels, young branchlets, and lower surface of upper leaves glabrous; southern California and northern Lower California ..... 3. *D. australis*, p. 58

Calyces swollen, expanding more or less above the tube into the throat which is typically somewhat contracted toward the summit; calyces, pedicels, young branchlets, and lower surface of upper leaves minutely pubescent; South Coast Ranges ..... 4. *D. lompocensis*, p. 62

b. Leaves not impressed-veiny above; corolla-tube usually exserted beyond the calyx-throat.

Corollas light lemon-yellow, ¾ to 1 inch broad, the lobes scarcely notched, distinctly recurved; calyces expanding abruptly above the narrow tube into a skirt-like throat and limb; southeastern San Diego County ..... 5. *D. aridus*, p. 63

Corollas warm buff to orange-yellow, 1½ to 2 inches broad, the lobes distinctly notched (variable in × *D. linearis*).

Leaves oblong-elliptic to elliptic, 1 to 2½ inches long, ¼ to ¾ inch wide; flowers 2¼ to 2¾ inches long; northern Sierra Nevada ..... 6. *D. grandiflorus*, p. 65

Leaves linear-oblong, ¾ to 2¼ inches long, ⅛ to ¼ or rarely to ½ inch wide; South Coast Ranges.

Flowers 1½ to 2¼ inches long ..... 7. *D. fasciculatus*, p. 70

Flowers typically 1 to 1½ inches long, but variable ..... 14. × *D. linearis*, p. 86

2. Calyces, lower leaf-surfaces, and upper branchlets visibly pubescent to woolly; pedicels about ¼ inch long.

Corollas light lemon-yellow, the tube usually exserted beyond the calyx-throat, the lobes commonly rotate; calyces usually abruptly flared above the tube, densely pubescent to woolly; inner South Coast Ranges, southern Sierra Nevada and southward ... 8. *D. calycinus,* p. 73

Corollas orange, orange-yellow, cream-colored to nearly white, the tube included, the three lower lobes extending forward, the two upper lobes extending at right angles or slightly recurved from the throat; middle South Coast Ranges, southward, and the islands off the coast of southern California ... 9. *D. longiflorus,* p. 76

B. Corollas red or shaded with red over yellow.

Pedicels typically 3/8 to 1 inch long, glabrous.

Leaves rarely as much as 3 or 4 times longer than broad, broadly elliptic, ovate, or oblanceolate; corolla-limb not over 3/4 inch broad, the lobes nearly equal and only slightly if at all notched, scarcely spreading; Santa Rosa, Santa Cruz, Anacapa, and San Clemente islands ... 10. *D. parviflorus,* p. 80

Leaves usually 3 or 4 times longer than broad, linear or linear-lanceolate to elliptic; corolla-limb 3/4 inch or more broad, the lobes unequal and slightly toothed or notched, distinctly spreading; southern California, northern Lower California and, in less typical form, on Santa Catalina Island ... 11. *D. puniceus,* p. 81

Pedicels typically less than 3/8 inch long.

Calyces, lower leaf-surfaces, upper branchlets, and pedicels distinctly glandular-hairy; southern California ... 12. *D. rutilus,* p. 83

Calyces, lower leaf-surfaces, upper branchlets, and pedicels not visibly hairy; corollas varying from red to yellow on the same plant or among plants of the same colony; southern California ... 11. *D. puniceus* × *D. australis,* p. 83

1. Diplacus Clevelandii (T. S. Brandg.) Greene. Cleveland Diplacus. Figs. 8, 25-1.

An erect freely branching perennial, 1 to 2 feet high, with herbaceous villous-pubescent and usually glandular-hairy stems

FIG. 8. *Diplacus Clevelandii* (T. S. Brandg.) Greene. (*Mimulus Clevelandii* T. S. Brandg.)

which are woody only at base. Leaves of two types: spring and early summer stem-leaves 1 to 3 inches long, 3/8 to 1 inch wide, lanceolate or oblong-lanceolate to elliptic, tapering to a broad sessile base, the upper surface yellow-green, distinctly impressed-veiny, finely hairy, the lower surface paler, distinctly hairy, often glandular, somewhat glutinous, the margin entire to usually toothed along the upper two-thirds, slightly to distinctly revolute; later summer and fall leaves much smaller, usually clustered on the lateral branches. Flowers borne singly in the axils of the main stem- and branch-leaves or on the smaller axillary branches which become naked in late summer and fall; pedicels 1/8 to 1/4 inch long, glandular-pubescent; calyx 3/4 to 1 1/4 inches long, the tube bulbous at base, constricted above the ovary and then expanding into a broader tubular-funnelform throat, glandular-hairy externally, becoming membranous in age and ultimately falling away from the fruit; corolla deep lemon yellow, 1 1/4 to 1 3/4 inches long, pubescent externally, the tube included, about 1/2 inch long, the throat expanding abruptly from the tube, about 3/4 inch long, with 2 rows of orange-colored dots internally on lower side, the limb with a dorso-ventral spread of 1 to 1 1/4 inches and a lateral spread of the 3 lower lobes of about 1 inch, the two upper lobes irregularly notched to nearly entire, slightly to distinctly recurved from the throat, the 3 lower lobes entire to finely toothed, extending forward away from the throat with only a slight curve; stamens included; style with stigma included. Capsule 3/8 to 1/2 inch long, somewhat quadrangular, when mature splitting at apex along 4 lines. Flowering period, May to July.

Distribution. Cleveland Diplacus is known in southern California from elevations of about 3000 to 6000 feet on Tecate, Guatay, Laguna, Cuyamaca, and Palomar mountains of San Diego County and in the higher elevations of the Santa Ana Mountains of Riverside and Orange counties. It occurs in dry soil, often in disturbed areas, along roadsides, and in the open borders of woods and chaparral.

Representative localities and specimens. California. San Diego Co.: Otay Mt., *F. F. Gander 2875* (SD); Tecate Mt. summit, *C. F. Harbison & Stoves* (SD 26023); high mountains near Descanso, *T. S. Brandegee* (UC 125167); Guatay Mt., Cuyamaca Quad., el. 4500 ft., *N. French 230* (UC–VTM); Laguna Mts., el. 4200 ft., *P. A. Munz 9758* (UC); hills e. of Pine Valley, *F. R. Fosberg 8437* (UC); Nigger Grade, Palomar Mt., "el. 4500 ft.?", *C. V. Meyer 492* (UC); Cuyamaca Peak, *T. S. Brandegee,* (G, isotype); Laguna Junction, *Epling, Darsie, Knox, Robison 107* (K, BM). Riverside Co.: Glen Ivy Trail to Santiago Peak, el. 4000 ft., *P. A. Munz 7062* (UC, P, G); along Indian Canyon Truck Trail, Santa Ana Mts., el. 3150 ft., *H. E. McMinn & M. Van Rensselaer 1897* (UC). Orange Co.: upper part of Indian Canyon Truck Trail, el. 4054 ft., near boundary between Riverside and Orange counties, *H. E. McMinn & M. Van Rensselaer 1898, 1899* (UC); Holy Jim Canyon to Santiago Peak, el. 3000 to 5200 ft., *P. A. Munz 7768* (P); Trabuco Peak, el. 4000 ft., Santa Ana Mts., *W. Pequegnat* (P 256712).

Type. ". . . on the south side of Cuyamaca Peak, . . . not far from the signal station on its summit," San Diego County, California, July 7, 1894, *T. S.*

Brandegee (UC 103634; isotypes, P 43251, G). "It grows in patches, spreading by underground roots [stems?] at . . . elevation over 6000 ft. . . ."

References. *Diplacus Clevelandii* (T. S. Brandg.) Greene, Erythea 4: 22 (1896). *Mimulus Clevelandii* T. S. Brandg., Gard. & For. 8: 134, fig. 20, p. 135 (1895).

2. Diplacus aurantiacus (Curt.) Jepson. Northern Diplacus. Orange Monkey-Flower. Figs. 9, 10.

An erect profusely branched shrub, often scraggly and the branches somewhat decumbent in age, 2 to 4 or rarely up to 8 feet high, with the stems, branches, and foliage puberulent to nearly glabrous but glandular and glutinous. Leaves 1 to 2 inches long, or longer on shaded plants and new growth, 1/4 to 5/8 inch wide, oblong-lanceolate or oblong-elliptic to nearly linear, the upper surface dark green, dull to shiny, distinctly impressed-veiny, nearly glabrous but glandular, the lower surface paler, usually with numerous simple and branched glandular and non-glandular hairs, the margin entire or denticulate to coarsely toothed, often revolute, the axils commonly with short branches bearing several smaller linear leaves. Pedicels 5/16 to 3/4 inch long, glandular-puberulent; calyx 3/4 to 1 1/4 inches long, tubular, only slightly and gradually broadening upward, glandular, glabrous to slightly pubescent with few scattered long thin hairs or short stout unicellular unbranched hairs; corolla deep orange to yellow-orange, 1 3/8 to 1 7/8 inches long, the tube 3/8 to 5/8 inch long, included, gradually enlarging upward into a funnelform throat 3/4 to 7/8 inch long, the limb with a dorso-ventral spread of 7/8 to 1 1/4 (1 1/2) inches and a lateral spread of the 3 lower lobes of 7/8 to 1 1/8 inches, the 2 upper lobes extending at right angles to or slightly bent forward or backward from the throat, laterally notched and entire to finely and irregularly toothed, the 3 lower lobes extending forward, mostly truncate or rounded, nearly entire to variously and shallowly notched or toothed; stamens with glabrous filaments, their anthers included or the 2 upper anthers slightly exserted; style with commonly exserted equal stigma-lobes. Capsule 5/8 to 7/8 inch long, opening along upper suture. Flowering period, March to July, or sometimes with a few flowers nearly throughout the year.

Distribution. Northern Diplacus inhabits rocky hillsides, cliffs, canyon-slopes, sometimes invading open forests, and borders of chaparral areas, from Coos County, Oregon, southward in the Coast Ranges of California to Santa Barbara County and in the Sierra Nevada from Placer County southward to Tuolume County. Forms intermediate between *D. fasciculatus* and *D. longiflorus* occur in the South Coast Ranges where these taxa overlap in their distribution. (See *D. fasciculatus* and *D. longiflorus*). In the inner South Coast Ranges of Stanislaus and San Benito counties and other extremely dry situations, the plants are more glandular-pubescent on the upper stems and calyces, thus approaching *D. longiflorus*.

FIG. 9. *Diplacus aurantiacus* (Curt.) Jepson. (*Mimulus aurantiacus* Curt.)

Representative localities and specimens. Coast Ranges. Oregon. Coos Co.: near Stout Memorial Park, *M. A. Radcliffe* (D 298707). Curry Co.: rocky seaward slopes near Brookings, *J. W. Thompson 12540* (UC, MO, G); 3 mi. n. of Brookings, *Doris Kildale 6999* (D). California. Del Norte Co.: at Douglas Park on Smith River, *J. W. Thompson 12932* (MO). Humboldt Co.: 1½ mi. sw. of Orick, el. 500 ft. (pedicels and upper branchlets glandular-pubescent), *G. T. Nordstrom 1437* (UC–VTM); hills s. of Ferndale, *A. E. Wieslander 217* (UC–VTM). Mendocino Co.: 7 mi. above mouth of Navarro River in *Sequoia sempervirens* forest (branches decumbent), *L. Constance 2512* (UC); near Ukiah, *Carl Purdy* (UC 26687). Sonoma Co.: along road from Kenwood to Oakville, *H. E. McMinn 5454* (UC); head of Hooker Canyon, *J. B. Spring 69* (UC–VTM). Lake Co.: 3½ mi. sw. of Upper Lake, el. 2100 ft., *K. Bradshaw 93* (UC–VTM); Mt. Konocti, el. 3000 ft., *J. W. Blankenship* (MO 997168). Marin Co.: Mt. Vision, *H. E. McMinn 5528* (UC); Muir Woods, el. 450 ft., *N. French 637* (UC–VTM); near Bolinas, *M. T. Doutt 143* (CM), pedicels up to ½ inch long. Solano Co.: Gates Canyon, near Vacaville, *A. A. Heller & H. E. Brown 5388* (P). Napa Co.: White Sulphur Springs, St. Helena, *H. P. Chandler 7588* (UC). San Francisco Co.: Mt. Davidson, *Ynez Windblad* (CA 308314). Contra Costa Co.: Mt. Diablo, inside of State Park along road from Danville, *H. E. McMinn 5455* (UC). Alameda Co.: se. side of Redwood Ridge, *L. Constance 471* (UC); Oakland hills n. of Mills College, *H. E. McMinn 5456* (UC); on cliffs between Tesla and Corral Hollow, *Roxana Ferris 7881* (UC); Cedar Mt., *A. D. E. Elmer 4355* (MO). Santa Clara Co.: western side of Mt. Hamilton Range, el. 2000 ft., *H. K. Sharsmith 1390* (UC); foothills near Stanford, *C. F. Baker 280* (UC). Stanislaus Co.: 9 mi. above mouth of Arroyo del Puerto, el. 1200 ft., *H. K. Sharsmith 1649* (UC). San Mateo Co.: Kings Mt., *E. W. Rust 127* (UC–Cl); halfway up La Honda Grade, *C. B. Wolf 1804* (UC). Santa Cruz Co.: near Santa Cruz, *M. E. Jones 2250* (P), (long internodes, large, toothed leaves, and pedicels up to 2 inches long); ¾ mi. ne. of Glenwood, el. 1600 ft., *W. W. Akey 76* (UC–VTM). San Benito Co.: 5 mi. e. of Paicines, on road to Panoche, el. 1600 ft. (glandular-pubescent form), *H. E. McMinn 5529* (UC); Pinnacles National Monument, *J. T. Howell 4607* (CA). Monterey Co.: Point Lobos State Park, *E. Lee & H. L. Mason 9203* (UC); near Big Sur P. O., *H. E. McMinn* (UC) (hybrid series with *D. fasciculatus 5481–5484*); open pine forest, Pacific Grove, *S. B. Parish 11502* (MO) (pedicels ⅜ to 1⅞ inches long). San Luis Obispo Co.: 1 mi. s. of Indian Knob, Arroyo Grande Quad., el. 350 ft., *H. C. Lee 387* (UC–VTM); Hazard Canyon, *H. E. McMinn 4351* (UC). Santa Barbara Co.: Harris Grade to Lompoc, *H. L. Mason 387* (UC); same locality, *H. E. McMinn 3853* (UC); 5 mi. s. of Surf, ½ mi. from sand dunes, *Roxana Ferris 7581* (D, UC, P); Point Sal, *Ralph Hoffman* (SM 11485). These Santa Barbara County specimens are very closely related to *D. lompocensis*.

Sierra Nevada. California. Tuolumne Co.: s. side of Stanislaus River, ca. 4 mi. n. of Columbia, *H. E. McMinn 5606, 5607, 5608* (UC); in chaparral above Indian Creek, el. 1200 ft., *Mrs. W. J. Williamson* (P 21011). Calaveras Co.: near Burson, el. 500 ft., in gravel on railroad embankment, *E. E. Stanford 2239* (P). Amador Co.: Ione hills, with *Arctostaphylos myrtifolia, H. E. McMinn 5514* (UC); ½ mi. se. of Ione, el. 500 ft., *R. D. Roseberry 551* (UC–VTM); 2¼ mi. nw. of Sugarloaf Peak, *G. T. Nordstrom 693* (UC–VTM). Eldorado Co.: "decumbent shrub, 2–3 ft. high", 3.8 mi. s. of Eldorado, *L. Constance 2473* (CA, UC, MO, P); South Fork American River, near Coloma, *H. E. McMinn 5515* (UC). Placer Co.: near Rattlesnake Bridge, Sacramento Quad., el. 300 ft., *N. French 44* (UC–VTM). Sacramento Co.: American River, bridge at Folsom, Lot 7, *H. E. McMinn* (UC). Stanislaus Co.: Knights Ferry, *F. W. Bancroft* (UC 26693).

Type. "Port Trinidad, California", 1792–1794, *Menzies* (BM and Acad. Nat. Sci. Philad.; these specimens good matches, both marked "Type"). On the back of the British Museum sheet is an annotation: "1. Hort. Kew 1795 ex California 2. California at Port Trinidad, M. Menzies." (Fig. 10.)

References. *Diplacus aurantiacus* (Curt.) Jepson, Man. p. 919 (1925).

FIG. 10. Type of *Diplacus aurantiacus* (Curt.) Jepson. (*Mimulus aurantiacus* Curt.) Specimen at the British Museum of Natural History.

Mimulus aurantiacus Curt., Bot. Mag. 10:1. 354 (1796). Colored plate opposite page of description. "Flowers . . . nearly twice the size of those of (M.) ringens, uniformly pale orange."; Grant in Ann. Mo. Bot. Gard. 11:338 (1924).

Mimulus glutinosus Wendl., Bot. Beobacht. 51 (1798); Jacq. Hort. Schoenber 3: pl. 364 (1798); Benth., Scroph. Ind. 28 (1835); Hook. & Arn., Beechey's Voyage, 154 (1841); Gray, Bot. Calif. 1:565 (1876), and Syn. Fl. N. Am. 2:275 (1878), ed. 2, and Suppl. 442 (1886).

Mimulus glutinosus Willd., Sp. Pl. 3: pars 1, 361 (1800). Name only.

Mimulus viscosus Moench, Suppl. ad Meth. pl. Hort. Marburg, 168 (1802).

Diplacus latifolius Nutt., Mss. (Oct. 12, 1837); Taylor's Ann. Nat. Hist. 1: no. 2, 138 (1838); Curtis, Bot. Mag. new ser. 12: under pl. 3655 (1838).

Diplacus leptanthus Nutt. (fig. 11) Mss. Oct. 12, 1837); Taylor's Ann. Nat. Hist. 1: no. 2, 138 (1838) as *Diplacus leptantha;* Curtis, Bot. Mag. new ser. 12: under pl. 3655 (1838), "Hab. California, Arch. Menzies, Esq. Described from specimens in the Herbarium of the Academy of Nat. Sciences of Philadelphia, which had been communicated by Sir Wm. Jackson Hooker to the late Dr. Schweinitz."

Diplacus glutinosus Nutt., Mss. (Oct. 12, 1837); Taylor's Ann. Nat. Hist. 1: no. 2, 138 (1838) as *Diplacus glutinosa;* Curtis Bot. Mag. new ser. 12: under pl. 3655 (1838); Benth., DC. Prodr. 10:368 (1846); Greene, Bull. Calif. Acad. Sci. 1:95 (1885), and in Pittonia 2:154 (1890).

Diplacus aurantius G. Don, Sweet Hort. Brit. ed. 3, 516 (1839). Name only, probably a misspelling for *aurantiacus.*

Diplacus glutinosus var. *aurantiacus* (Curt.) Lindl., in Paxt. Fl. Gard. 3: under pl. 92, opposite page 95 (1852–1853); Planchon, Fl. Des Serres et Des Jardins De L'Europe, Ann. Gen. D'Hort. 9; under pl. 883 (1853–1854). The colored plate no. 883 of *D. glutinosus grandiflorus,* facing p. 71, is *D. grandiflorus* (Lindl.) J. Grönl.

Diplacus glutinosus var. *latifolius* Greene, Pittonia 2:155 (1890).

3. **Diplacus australis** nom. nov. San Diego Diplacus. Fig. 12.

An erect profusely branched shrub, 1½ to 3 feet high, with glabrous or microscopically glandular-puberulent stems, branches, and leaves, the upper stems and branches often reddish. Leaves 1 to 2½ or rarely to 3½ inches long, ¼ to ⅝ inch wide, linear-lanceolate, oblong-elliptic to narrowly elliptic or lanceolate, the upper surface green, glabrous, somewhat impressed-veiny, the lower surface lighter green, glabrous, glutinous, the margin finely toothed or nearly entire, often revolute, the axils frequently with short branchlets bearing several smaller leaves. Pedicels 3/16 to ⅜ inch long, glabrous; calyx ¾ to 1¼ inches long, tubular or slightly expanding upward into the throat; corolla orange-yellow to light apricot or buff to nearly white, 1¾ to 2 inches long, the tube included, ⅝ to ¾ inch long, the throat funnelform, about ¾ inch long, the limb with a dorso-ventral spread of 1¼ to 1½ inches and a lateral spread of the 3 lower lobes of 1 to 1¼ inches, the 2 upper lobes with a lateral notch and usually with several small irregular teeth and extending at right angles or slightly recurving from the throat, the 3 lower lobes finely and irregularly toothed to nearly entire at their truncate tips, curving forward from the throat; stamens included; style with stigma included. Capsule about ½ inch long, opening along the upper suture. Flowering period, March to July.

FIG. 11. Type of *Diplacus leptanthus* Nutt. [*Diplacus aurantiacus* (Curt.) Jepson]. Specimen at the Philadelphia Academy of Natural Sciences.

Distribution. San Diego Diplacus is restricted to southernmost California and adjacent Mexico. It occurs on burned-over hillsides and otherwise disturbed areas and on granite cliffs, mainly in central and western San Diego County and at a few scattered localities in Orange and eastern Riverside counties and in northern Lower California. On Santa Catalina Island, plants intermediate between this entity and *D. puniceus* occur.

Representative localities and specimens. Lower California, Mexico: "In scant chaparral on hillsides 23 mi. s. of Ensenada," *I. L. Wiggins & D. Demaree 4707* (D, CA, UC, P, G) (calyx slightly glandular-puberulent); Johnson Ranch, San Antonio del Mar, *F. F. Gander 7348* (SD); near San Rafael, *C. R. Orcutt 1295* (MO, G). California. San Diego Co.: hills near Ysidora, *L. R. Abrams 3287* (NY, P, G); hills between Campo and Potrero, *L. R. Abrams 3716* (P, G); 15 mi. w. of Jacumba, between Newton and La Posta, *D. A. Johansen & J. A. Ewan 7162* (P); 2 mi. w. of Live Oak Springs, *F. F. Gander 5717* (SD); e. of Alpine, Highway 80, *H. E. McMinn 5595* (UC): ca. 6 mi. nw. of Boulevard, Highway 80, *H. E. McMinn 5596* (UC); Barrett Dam, *P. A. Munz 7993* (P); hillside ¾ mi. w. of Dehesa School, *F. F. Gander 5063* (SD): near se. base of El Capitan (El Cajon Mts.), *F. F. Gander 8448* (SD); ca. 3 mi. e. of Flinn Springs, *H. E. McMinn & M. Van Rensselaer 1906* (UC); Barona Valley, *F. F. Gander 2176* (SD); 5 mi. s. of Mesa Grande on Black Canyon Road, *F. F. Gander 2004* (SD); grade above Henshaw Dam, *F. F. Gander 6349* (SD); Ramona, *T. S. Brandegee* (UC 103642); Herron Ranch, near De Luz, *F. F. Gander 8260* (SD) (approaches *D. puniceus*); hills 2 mi. s. of San Onofre, *I. L. Wiggins 3021* (D, UC); San Diego, Calif., *D. Cleveland 6096* (MO). Orange Co.: about 2 mi. e. of San Juan Capistrano on San Juan Pass Road (Highway 74), *H. E. McMinn* (UC); 2 mi. e. of San Juan Hot Springs, *Alice Eastwood & J. T. Howell 3929* (CA); head of Silverado Canyon, Corona Quad., el. 3500 ft., *A. Lewis 365* (UC–VTM); Santiago Canyon, *H. M. Hall 9403* (UC) (in a series with *9404, 9405* constituting a hybrid swarm of *D. puniceus* × *D. australis*); Laguna Canyon, ca. 2 mi. ne. of Laguna Beach, *M. Van Rensselaer 1876* (UC), "Shrub about 7 ft. tall with trunk ⅝ inch in dia. at base." Riverside Co.: Indian Canyon Truck Trail to summit of ridge, Santa Ana Mts., el, 2800 ft., *H. E. McMinn & M. Van Rensselaer 1892, 1893* (UC) (belonging to a hybrid series of *D. longiflorus* × *D. australis*); San Juan Canyon, el. 1700 ft., Elsinore Quad., Sec. 1. T 7 S, R 6 W, *A. Lewis 407* (UC–VTM). Los Angeles Co.: foothills of Flint Ridge, Pasadena, *G. T. Hastings*, July 9, 1927 (NY).

Type. Descanso Grade, San Diego County, California, June, 1906, *Katherine Brandegee* (UC 126069).

References. *Diplacus australis* McMinn. This San Diego County entity has usually been considered as *D. longiflorus* var. *linearis* (Benth.) McMinn or *D. linearis* (Benth.) Greene. However, the name *linearis* is not tenable here because it was applied by Bentham to another and quite distinct entity from Monterey County. The name *D. australis* is here proposed for these more southerly plants.

Diplacus linearis (Benth.) Greene, Pittonia 2:156 (1890), as to specimens cited, location, and description but not as to type. The type of what Greene thought was *Mimulus linearis* Benth. is a Douglas specimen, fig. 24, collected very probably in Monterey County. It has narrow linear leaves which are not at all impressed-veiny above. After comparing the type specimen at the British Museum of Natural History and part of the type at the New York Botanical Garden, with abundant material in the field and garden, I am of the opinion that *D. linearis* (Benth.) represents one of the numerous hybrid forms between *D. aurantiacus* and *D. fasciculatus* found in Monterey County (see p. 87). Such hybrids occur along the Big Sur River and in the upper Carmel River Valley where Douglas was known to have collected. (See section on Natural Hybrids, *D. aurantiacus* × *fasciculatus*.)

FIG. 12. *Diplacus australis* McMinn.

Mimulus longiflorus var. *linearis* (Benth.), as misinterpreted by Grant, Ann. Mo. Bot. Gard. 11: 334 (1924). Not *M. linearis* Benth., Scroph. Ind. 27 (1835).

Diplacus longiflorus var. *linearis* (Benth.) McMinn, Ill. Man. Calif. Shrubs 498 (1939).

4. **Diplacus lompocensis** sp. nov. Lompoc Diplacus.

Herba erecto parce ramosa 3.5–10 dm. alta caulibus ramisque brunneis glabris vel paulo puberulis. Folia lineari-oblonga vel lanceolata vel elliptica 2.5–5 cm. longa 3–13 mm. lata supra atroviridia opaca vel nitida impresso-venosa glabra indumento glanduloso obtecta subtus pallidiora pilis simplicibus ramosisque obsita marginibus integris vel glanduloso-denticulatis aspectu aestivali auctumnalique plerumque revolutis. Flores palide aurantio-lutei pedicellis 3–7 mm. longis minutissime glanduloso-puberulis calycibus minute glanduloso-puberulis basi tubulatis 18–28 mm. longis ad os versus in faucem tumidam demum ad apicem versus paulo angustatam dilatatis corollis 3.5–5 cm. longis tubo incluso plus minusve 12 mm. longo in faucem infundibuliformem 18–25 mm. longam aliquanto abrupte ampliato limbo recte 28–38 mm. metiente lobis tribus inferioribus productis plerumque apicibus truncatis dentibus irregularibus duobus usque ad sex instructis late 28–32 mm. metientibus lobis duobus superioribus a latere incisis ceterum integris vel irregulariter dentatis ex apice recte divergentibus vel paulo recurvatis filamentis glabris antheris inclusis stylo glandulis stipitatis instructo eius lobis subaequalibus in corollae fauce inclusis. Capsula per suturam dorsalem dehiscens.

An erect sparsely branched shrub, 1 to 3 feet high, with brown, glabrous to slightly puberulent stems and branches. Leaves 1 to 3 inches long, 1/8 to 3/4 inch wide, linear-oblong, lanceolate, or elliptical, the upper surface dark green, dull to shiny, impressed-veiny, glabrous, glandular, the lower surface paler, with simple and branched glandular pubescence, the margin entire to glandular-denticulate, commonly revolute in the summer and fall foliage. Pedicels 1/8 to 5/16 inch long, microscopically glandular-puberulent; calyx 3/4 to 1 1/8 inches long, tubular at base, expanding upward into a swollen throat which becomes somewhat contracted toward apex, minutely glandular-puberulent; corolla light orange-yellow, 1 1/2 to 2 inches long, the tube about 1/2 inch long, included, rather abruptly enlarged into a funnelform throat 3/4 to 1 inch long, the limb with a dorso-ventral spread of 1 1/8 to 1 1/2 inches and a lateral spread of the 3 lower lobes of 1 1/8 to 1 1/4 inches, the upper 2 lobes extending at right angles or slightly recurved from the throat, laterally notched and entire to irregularly toothed, the lower 3 lobes extending forward, mostly truncate and with 2 to 6 irregular teeth at apex; stamens with glabrous filaments, their anthers included; style with minute stipitate glands, the stigma-lobes subequal, included within the throat of corolla. Capsule 5/8 to 7/8 inch long, opening

along the upper suture. Flowering period, March to July.

Distribution. Lompoc Diplacus occurs in a limited coastal area on the chaparral-covered slopes of Lompoc Mesa and adjacent low hills in Santa Barbara County, California, in extreme southern San Luis Obispo County, and probably in western Ventura County. It occupies a region situated at the southern distribution of *D. aurantiacus* and at the northern distribution of the major populations of *D. longiflorus*. Many of its characteristics are intermediate between these two taxa. (See Biological Relationships.)

Representative localities and specimens. California. Santa Barbara Co.: road bank, edge of open woodland, along Highway 1 from Lompoc to Las Cruces, *H. E. McMinn 5601* type, *5602, 5614* (UC); Lompoc Mesa, *H. E. McMinn 5612, 5613, 5618, 5619, 5620* (UC); sandy bushy slope, 400 ft. el., n. of Mission La Purisima, ne. of Lompoc, *F. W. Pennell 25338* (UC); Gaviota Pass, *L. R. Abrams 5033* (D, P); 3½ mi. s. sw. of Harris, el. 800 ft., *H. C. Lee 285* (UC–VTM); 4 mi. w. of Lompoc, el. 500 ft., *G. E. Sindel 191* (UC–VTM); Purisima Hills between Lompoc and Harris Grade, *Roxana Ferris 7540* (UC); San Julian Ranch, *Ralph Hoffman* (SM 11488). San Luis Obispo Co.: Cayucos Quad., Sec. 20, T 30S, R 11 E, el. 150 ft., *B. Bolt 533* (UC–VTM). Ventura Co.: ½ mi. n. of mouth of Modelo Canyon, Piru Quad., Sec. 16. T 4N, R 18W, el. 1000 ft., *A. D. Gifford 19* (UC–VTM) (close to *D. lompocensis* but probably *D. longiflorus*); Cary Dell Trail (Ventura River basin), *Henry M. Pollard* (SM 19616), very close to *D. lompocensis*.

Type. At edge of open woods along Highway 1 from Lompoc to Las Cruces, Santa Ynez Mts., Santa Barbara County, California, June 7, 1949, *H. E. McMinn 5601* (UC 914709).

Reference. *Diplacus lompocensis* McMinn.

5. Diplacus aridus Abrams. Jacumba Diplacus. Fig. 13.

A low decumbent subshrub, 8 to 18 inches high, with a spread of 2 to 4 feet, usually with straw-colored stems and branches and glabrous glutinous herbage. Leaves ¾ to 1¾ or rarely 2½ inches long, ¼ to ⅞ inch wide, narrowly to broadly elliptic or rarely lanceolate to oblanceolate, the surface yellowish green, glabrous, glutinous, the margin slightly toothed, often apparently entire because of a tendency to become revolute. Pedicels ⅛ to ¼ inch long, glabrous; calyx 1 to 1¼ inches long, funnelform, the upper one-third to one-half distinctly flared, glabrous; corolla light lemon- or golden-yellow, 1½ to 2 inches long, the tube exserted, ¾ to 1¼ inches long, the throat abruptly expanding from the tube, broadly funnelform, ½ to ⅝ inch long, the limb rotate, with a dorso-ventral spread of ¾ to 1 inch and a lateral spread of the 3 lower lobes of ¾ to 1 inch, all the lobes spreading at right angles to the throat and usually recurved, rounded, only slightly toothed to entire; stamens included or the upper 2 with anthers slightly exserted; style with stigma exserted. Capsule ½ to ¾ inch long, splitting along the upper suture. Flowering period, April to July.

Distribution. Jacumba Diplacus is known only from the dry hills and ridges of southeastern San Diego County and in adjacent

Lower California. It has been collected in scattered localities from Tecate, Lower California, eastward and northward in California to the desert slope of the Laguna Mountains between Shaw

Fig. 13. *Diplacus aridus* Abrams.

and Potrero canyons. The lemon-yellow, rotate corollas with exserted tubes and flared calyces characteristic of this entity also appear in plants from central-northeast San Diego County. These plants, however, have considerable fine to woolly pubescence and are treated under *D. calycinus*.

Representative localities and specimens. Lower California, Mexico. Tecate, "between great granite rocks in chaparral," el. ca. 1850 ft., *F. R. Fosberg 8439* (P). California. San Diego Co.: dry ridges, Jacumba, *L. R. Abrams 3656*

(D, G, MO, NY, P, UC, K, BM); among rocks near the boundary monument, Jacumba, *H. E. McMinn 4006* (UC); se. slope of high boulder covered ridge, Jacumba Mts., overlooking Carrizo Gorge, about 5 mi. (airline) ne. of Jacumba and about 1½ miles ne. of Dubber, *M. Van Rensselaer 1871* (UC); desert slope of Laguna Mts., between Shaw and Potrero canyons, *C. F. Harbison 1939* (SD); 5 mi. w. of Jacumba at Bankhead Springs, among rocks north of highway, el. 3400 ft., *C. B. Wolf 2199* (D, UC); Boulevard, *F. F. Gander 5691* (SD); Deer Springs, Hipass, *M. L. Harris* (SD 21395); rocky ridge about 150 ft. n. of Jacumba boundary (Mexico) monument, ¼ mi. sw. of community of Jacumba, *M. Van Rensselaer 1868* (UC), "Single stem 39 inches long, growing in sheltered spot, leaf 2½ × 1½ inches."

Type. "Growing on dry rocky ridges at Jacumba, near the boundary monument," San Diego County, California, May 31, 1903, *L. R. Abrams 3656* (NY: isotypes D, G, P, MO, UC).

References. *Diplacus aridus* Abrams, Bull. Torr. Bot. Club 32: 540 (1905). "The peculiar calyx and long slender corolla-tube, as well as the pattern of the lobes, readily distinguish this species from all other members of the genus."

Mimulus aridus (Abrams) Grant, Ann. Mo. Bot. Gard. 11: 336 (1924).

6. Diplacus grandiflorus (Lindl.) J. Grönl. Azalea-flowered Diplacus. Northern Sierra Diplacus. Figs. 14, 15, 16, 17.

A spreading subshrub, ¾ to 2½ or rarely to 4 feet high, with a spread of 1 to rarely 3 feet, the branches and foliage glabrous, microscopically glandular-puberulent, densely covered in late spring and early summer with Azalea-like flowers. Leaves 1 to 2½ inches long, ¼ to ¾ inch wide, oblong-elliptic to elliptic, the upper surface dark green, glabrous, not impressed-veiny, the lower surface lighter green, glabrous, glutinous, the margin entire or slightly toothed, commonly slightly revolute, the lower and larger leaves sometimes with axillary clusters of smaller leaves. Flowers numerous; pedicels ¼ to ⅜ inch long, microscopically glandular-puberulent; calyx 1⅛ to 1¼ inches long, tubular, or the throat gradually expanding from the basal tubular portion; corolla buff or cream-colored, 2¼ to 2¾ inches long, the tube commonly slightly exserted, about 1 inch long, the throat funnelform, about 1 inch long, gradually or abruptly expanding upward from the tube, the limb with a dorso-ventral spread of 1½ to 2 inches and a lateral spread of the 3 lower lobes of 1½ to 1¾ inches, the 2 upper lobes with a broad deep lateral notch and sometimes with a few smaller notches, spreading at right angles or slightly recurved from the throat, the 3 lower lobes with a deep median notch and often with a few irregular and smaller notches, curving forward from the throat; stamens included; style with stigma included or slightly exserted. Capsule ½ to ⅝ inch long, opening along the upper suture. Flowering period, April to July.

Distribution. Azalea-flowered Diplacus occurs on granite cliffs and rocky outcroppings of the western slope of the Sierra Nevada in the drainage basins of the Feather, Yuba, and Bear rivers of Plumas, Butte, Yuba, Sierra, Nevada, and Placer counties, California. One locality, Cape Horn near Colfax, is in the drainage basin of the North Fork of the American River. It in-

FIG. 14. *Diplacus grandiflorus* (Lindl.) Grönl. (*Diplacus glutinosus* var. *grandiflorus* Lindl.)

FIG. 15. Four seedlings of *Diplacus grandiflorus,* left; four seedlings of *D. fasciculatus,* right.

habits the areas adjacent to the river canyons and is rarely found on the upper flats between the rivers or their branches.

Representative localities and specimens. California. Plumas Co.: Belden, *W. L. Jepson 4450* (UC-J); from Pulga to Belden, *H. E. McMinn*, Aug., 1949. Butte Co.: w. slope of Sierra Nevada between Chico and Forest Ranch, el. 2000 ft., *A. A. Heller 11407* (MO, NY, UC); hills e. of Chico, *Mrs. R. M. Austin 161*

Fig. 16. Three young plants of *Diplacus grandiflorus*, right; three young plants of *D. fasciculatus*, left.

(UC); Feather River Canyon, 5 mi. e. of Oroville, el. 500 ft., *Lewis S. Rose 33186* (CA), also ca. 9 mi. e. of Oroville, *H. E. McMinn 5503* (UC); North Fork Feather River, 3 mi. s. of Pulga, el. 2000 ft., *Lewis S. Rose 39242* (G, NY). Yuba Co.: North Fork Yuba River, road from Dobbins to Camptonville, *H. E. McMinn 5507* (UC); Middle Fork Yuba River, n. of North San Juan, *H. E. McMinn 5509* (UC); 4 mi. nw. of North San Juan, el. 1400 ft., *L. Constance 2291* (UC); Smartsville, *Mrs. J. E. Cramsie* (CA 28305). Sierra Co.: 4½ mi. w. of Sierra City, el. 3500 ft., Downieville Quad., *A. Lewis 525* (UC–VTM) (pedicels of fruit up to 1 inch long); Cedar Glen, *Vincent Jones* (CA 28317). Nevada Co.: South Fork Yuba River, ca. 5 mi. nw. of Nevada City, *H. E. McMinn 5510* (UC); Nevada City, *Chas. W. Kitts* (UC 445118); Smartsville Quad. Sec. 27 T 17N, R7E, *R. W. Lundh 251* (UC–VTM) (pedicels ¼ to ½ inch long). Placer Co.: 1 mi. w. of Lake Spaulding, el. 4800 ft., *N. French 376* (UC–VTM); among rocks ca. 1½ mi. w. of Lake Spaulding, ca. 400 yds.

FIG. 17. Mature garden-grown plants: *Diplacus grandiflorus,* upper; *D. fasciculatus,* lower.

from Bear River Bridge, e. end of Bear Flats, above flume, *H. E. McMinn 5501, 5502* (UC); near Cape Horn, *K. Brandegee* (UC 112831), June 5, 1908, and *C. F. Sonne* (UC 445119), June 17, 1891 (Colfax Quad.).

Type. From a plant cultivated in England. "A Greenhouse evergreen Shrub, from California . . . now figured with pale salmon-colored flowers, the lobes of which are deeply cleft, and the leaves rather shorter than usual, and less serrated." (Paxton's Flower Garden 3: 95–96, colored plate 92, opposite page 95, 1852–1853). This plate is a very satisfactory reproduction of the plants from the Feather River Canyon, California.

References. *Diplacus grandiflorus* (Lindl.) J. Grönl., Paris Revue Horticole IV, 6: 402 404, fig. 136, p. 403, not colored (1857). The figure (136) is a good reproduction of plants from the Sierra Nevada. ". . . distincts toutefois du Diplacus glutinosus ordinaire, principalement par la grandeur des fleurs et par la division profonde des cinq lobes de la corolle . . ."

The plants referred to in this paper as the binomials *D. grandiflorus* (Lindl.) J. Grönl. and *D. fasciculatus* (Pennell) McMinn have often been known as *D. leptanthus*. That name, however, was given by Nuttall, in 1837, to another distinct entity which, because of rules of nomenclature with regard to priority, is now known as *D. aurantiacus*.

Many botanists, including myself, had considered the plants of the Sierra Nevada, *D. grandiflorus*, and those of Monterey County, *D. fasciculatus*, to be the same taxon. Dr. H. L. Mason suggested to me as early as 1932 that they appeared to him to be quite distinct. Dr. F. W. Pennell (1947) also considered them distinct when he described the Monterey County entity as a new subspecies, *Mimulus bifidus fasciculatus*. After extensive field, garden transplant, and seedling studies (figs. 15, 16, 17) I am convinced that the plants should be treated as two distinct entities.

Diplacus glutinosus var. *grandiflorus* Lindl. in Paxton's Flower Garden 3: 95–96, colored plate 92 opposite page 95 (1852–1853). "That now figured has been raised in many places within the last few months, and has already gained the false name of *D. leptanthus*, a plant to which it bears very little resemblance. . . . That now figured is certainly much the finest, on account of its large pale salmon-colored flowers; a cross between which and *puniceus* ought to be very handsome."

Diplacus glutinosus grandiflorus Planchon, Flore Des Serres et Des Jardins De L'Europe, Annales Générales D'Horticulture, Tome IX, colored plate 883 facing p. 71 (1853–1854). This plate is a good reproduction of the Sierra Nevada plants. "Le *Diplacus glutinosus, grandiflorus* a déjà reçu, parait-it dans quelques jardins le nom faux de *Diplacus leptanthus*, c'est-a-dire d'une espece a feuilles plus étroites, plus petites et plus fermes, indigène dans la Californie, comme le glutinosus lui-meme, et probablement connue des seuls botanistes." J. E. Planchon.

Diplacus longiflorus, as misinterpreted by Greene, as to the northern Sierra Nevada plants only. Bull. Calif. Acad. Sci. 1: 96 (1885). Not Nuttall.

Diplacus grandiflorus Greene, Pittonia 2: 156 (1890), as to the Sierra Nevada plants only.

Mimulus leptanthus (Nutt.) Grant, in Gentes Herb. 1: 136 (1923), and in Ann. Mo. Bot. Gard. 2: 335 (1924), as to Sierra Nevada plants only.

Diplacus longiflorus var. *grandiflorus* (Grönl.) Jepson, Man. 919 (1925), second printing. Sierra Nevada plants.

Diplacus leptanthus as misapplied by McMinn, Ill. Man. Calif. Shrubs 499 (1939), as to Sierra Nevada plants only. Not Nuttall.

Mimulus bifidus Pennell, Proc. Acad. Nat. Sci. Phil. 99: 168 (1947). New name for *Diplacus grandiflorus* J. Grönl., (1857). Preoccupied in *Mimulus* by *M. grandiflorus* Howell (1901).

7. **Diplacus fasciculatus** (Pennell) comb. nov. Santa Lucia Diplacus. Figs. 18, 15, 16, 17.

An erect or spreading subshrub, 1 to 2½ feet high, with

FIG. 18. *Diplacus fasciculatus* (Pennell) McMinn. (*Mimulus bifidus* subsp. *fasciculatus* Pennell.)

glabrous microscopically glandular-puberulent stems and foliage, the main stems erect. Leaves ¾ to 1½ inches long, ⅛ to ¼ or rarely ½ inch wide, linear or linear-oblong to narrowly elliptic, the upper surface dark green, glabrous, not impressed-veiny, the lower surface lighter green, glabrous, the margin entire or finely toothed along upper half, commonly revolute, the axils of the larger stem-leaves usually bearing short lateral branchlets with several smaller leaves. Pedicels ¼ to ⅜ or rarely to ½ inch long, glabrous; calyx 1⅛ to 1¼ inches long, tubular, scarcely expanding upward; corolla buff to orange-buff, 1¾ to 2¼ inches long, the tube usually slightly exserted, about ¾ inch long, the throat funnelform, ¾ to ⅞ inch long, the limb with a dorso-ventral spread of 1¼ to 1¾ inches and a lateral spread of the 3 lower lobes of 1¼ to 1⅜ inches, the 2 upper lobes with a deep lateral notch and with 1 or more smaller and irregular serrations, extending at right angles or slightly forward from the throat, the 3 lower lobes with a deep median notch and often with 1 to 3 smaller notches, extending forward from the throat; stamens included; style with stigma included. Capsule ½ to ⅝ inch long, splitting along upper suture. Flowering period, April to July.

Distribution. Santa Lucia Diplacus occurs in the central Coast Ranges of California on rocky outcroppings of banks and in washes from the upper Carmel River Valley of Monterey County southward through the Santa Lucia Mountains to southwest of Templeton in San Luis Obispo County, and at the Pinnacles National Monument in San Benito County.

Representative localities and specimens. California. San Benito Co.: wash into Chalone Creek, Pinnacles National Monument, *H. E. McMinn 5530, 5531* (UC); ca. 200 yds. inside of Pinnacles National Monument entrance, *H. E. McMinn 5465, 5478* (UC) (in broad spreading clumps). Monterey Co.: upper Carmel River Valley, *H. E. McMinn 5519* (UC); between Pineys and Jamesburg, on a branch of Arroyo Seco, *H. E. McMinn 2665* (UC); ca. 24 mi. w. of King City, along Memorial State Park Road from King City to the Indians, el. 1400 ft., *H. E. McMinn 5542* (UC); also ca. 39 miles from King City, headwaters of Arroyo Seco, 2 mi. n. of camp ground on rocky outcropping near bridge, el. 2200 ft., *H. E. McMinn 5543* (UC); grade about 3 mi. above Tassajara Hot Springs, el. 2800 ft., *Roxana Ferris & R. Bacigalupi 8327* (D, P, UC); also *H. E. McMinn 5604, 5605* (UC); bank of the San Antonio River, *H. L. Mason 5767* (UC); 1.3 mi. se. of Berry Ranch, el. 1300 ft., *A. Simontacchi 617* (UC-VTM); near Big Sur P. O., *Roxana Ferris & R. Bacigalupi 3704* (D, P); Big Sur River, *Arthur J. Bolton* (P, *Baker 5101*) (calyces slightly puberulent); Burro Trail, e. slope of Santa Lucia Mts. between Jolon and Gorda, *K. Brandegee* (UC 130960). San Luis Obispo Co.: 7.3 mi. w. of Paso Robles on Adelaida Road, el. 1620 ft. (flowers with more orange and less bifid lobes), *H. E. McMinn 5554* (UC) (some plants with pubescent calyces and deep orange corollas, thus with genes from *D. aurantiacus* and *D. longiflorus*); common on rocky outcroppings from Adelaida to Nacimiento River, *H. E. McMinn;* 3½ mi. sw. of Templeton, el. 1600 ft., *H. C. Lee 891* (UC–VTM).

Type. ". . . on rocky hills, Santa Lucia Park, Arroyo Seco, at 2,500 feet altitude, Monterey County, California," May 10, 1931, *Lewis S. Rose 32678* (Acad. Nat. Sci. Phil.).

References. *Diplacus fasciculatus* (Pennell) McMinn. See references for *Diplacus grandiflorus,* p. 70.

Mimulus bifidus subsp. *fasciculatus* Pennell, Proc. Acad. Nat. Sci. Phil. 99: 168 (1947).

Mimulus glutinosus var. *linearis* Gray, Proc. Am. Acad. 11: 97 (1876), in part.

Diplacus grandiflorus Greene, Pittonia 2: 156 (1890), as to Monterey County plants only. Not J. Grönland.

Mimulus leptanthus Grant, Gentes Herb. 1: 136 (1923) and Ann. Mo. Bot. Gard. 2: 235 (1924), as to Monterey County plants only, not *Diplacus leptanthus* Nutt.

Diplacus leptanthus as misapplied by McMinn, Ill. Man. Calif. Shrubs 499, not Nuttall, as to Monterey County plants only.

8. Diplacus calycinus Eastw. Woolly Diplacus. Fig. 19.

A semi-erect or spreading irregularly branched subshrub, 1 to 2 feet high, with light brown or straw-colored branches, commonly densely woolly on upper parts. Leaves 1¼ to 2¼ or rarely 4 inches long, ⅜ to 1 or rarely 1⅜ inches wide, oblong-elliptical, obovate, lanceolate, or oval, the upper surface yellow-green, glabrous, somewhat impressed-veiny, the lower surface glandular, with simple and branched hairs, the margin entire to finely toothed along the upper two-thirds, commonly revolute, the axils often with short branches bearing several smaller leaves. Pedicels 3/16 to ⅝ inch long, densely glandular-villous with mostly simple hairs; calyx 1 to 1⅜ inches long, tubular in lower half, then abruptly expanding and distinctly flared, densely glandular-villous to woolly, with simple and branched hairs; corolla light lemon-yellow, 1¾ to 2½ inches long, the tube exserted or rarely included, 1 to 1⅜ inches long, the throat funnelform, commonly abruptly expanding from the tube, ⅝ to ¾ inch long, the limb nearly rotate, with a dorso-ventral spread of 1 to 1¼ inches and a lateral spread of the 3 lower lobes of ⅞ to 1¼ inches, the 2 upper lobes with a deep lateral notch and irregularly toothed to nearly entire, the 3 lower lobes truncate or rounded and entire to finely toothed at their tips; stamens included or the 2 upper with anthers nearly exserted; style with stigma exserted. Capsule ½ to ¾ inch long, opening along the upper suture. Flowering period, April to July.

Distribution. Woolly Diplacus inhabits rocky outcroppings of the lower and middle slopes of three distinct, yet geographically related, mountain areas; the southern Sierra Nevada, the eastern portions of the mountains of southern California, and the inner South Coast Ranges, California. In the southern Sierra Nevada, it occurs from near Trimmer Springs, Fresno County southward through Tulare County to near Caliente, Kern County.

A. A. Heller states that this species was, "Common in the Tehachapi Mts., on steep northerly slopes in damp places" (*Heller 7771*, MO 92467). I have been unable to verify this distribution either in the field or from herbarium specimens. It appears that during the past 50 years the north slopes of the Tehachapi Mountains have become increasingly dry and consequently now are not

suitable for the growth of this taxon. This formerly, more continuous distribution would help explain the present relict distribution of *D. calycinus* in the inner South Coast Ranges of San Luis Obispo County.

In southern California, it occurs from the North Fork of San Antonio Canyon in the extreme eastern end of the San Gabriel Mountains eastward on the northern face of the San Bernardino Mountains to near Quail Springs in the Joshua Tree National Monument of San Bernardino and Riverside counties and southward in the San Jacinto Mountains to the mountains of central northeast San Diego County. In the South Coast Ranges it occurs on the eastern slopes of the Pozo Mountains in San Luis Obispo County. On the western slope of the Pozo Mountains, it merges with *D. longiflorus* and in southeastern San Diego County it is replaced by *D. aridus*. (See section on Biological Relationships.)

Representative localities and specimens. California. Fresno Co.: Base Camp, junction of North and South forks Kings River, *W. B. Duncan* (D 125326); above Trimmer Springs, *Ynez Winblad* (CA 258704—calyces less woolly); Tehipite Valley, el. 4000 ft., *H. M. Hall & H. P. Chandler 511* (CM, MO, UC) (close to *D. longiflorus*); South Fork Kings River, el. 3600 ft., up and down canyon for 7 mi. by bridge at Boyden Caves, *H. E. McMinn 5517* (UC) (some calyces more glandular-pubescent than woolly). Tulare Co.: hills e. of Orosi, *R. F. Hoover 3474* (UC) (leaves much more glabrous than in typical forms); Grapevine Spring, about 35 mi. e. of Visalia, *P. S. Woolsey* (UC 26695); South Fork Kaweah River, *Culbertson 4407* (G, K, MO, NY, P, UC); road to Camp Nelson, between it and junction of road to Camp Wishon, el. 3600 ft., *R. Bacigalupi, I. L. Wiggins, & Roxana Ferris 2660* (D, UC) (a very villous form); White River Road, *Lester Rowntree* (CA 308308); canyon of South Creek, Kern River Canyon, about 2 mi. se. of Johnsondale sawmill, el. 3900 ft., *R. Bacigalupi & Roxana Ferris 2458* (D); Sequoia Nat. Park, *W. T. Frost* (UC–VTM 7599). Kern Co.: Glennville, *E. Roy Weston 132* (CA); Greenhorn Mt., *Mrs. E. C. Van Dyke* (CA 191496); along highway, 2 mi. e. of Weldon, *E. W. Voegelin 174, 276* (UC) (tube scarcely exserted); Greenhorn Mt. Range, rocky cliff, el. 1200 ft., *Lyman Benson 2934* (P, UC) (leaves scarcely hairy, resembling somewhat *D. aridus*); Kern River Road, 15 mi. from Bakersfield, el. about 1500 ft., steep woody canyon slope, *Frank W. Peirson 7309* (P) (stems very hairy); between Keene and Bealville, *K. Brandegee* (UC 130959); Caliente, *T. S. Brandegee* (UC 124421); lower Kern River Canyon, 4 mi. from mouth, *L. R. Abrams 12007* (D, UC–Cl.) (calyces very villous, leaves broad and quite hairy); Kern Canyon, *A. A. Heller 7771* (MO 92467-*D. latifolius* Nutt. Ann. & Mag. Nat. Hist. 1: 137, 1838). San Bernardino Co.: North Fork San Antonio Canyon, San Antonio Mts., el 7500 ft., *I. M. Johnston 1607* (UC); ½ mi. sw. of junction of Deep Creek and Mohave River, el. 3500 ft., *D. Axelrod 64* (UC-VTM); 1.5 mi. se. of mouth of Deep Creek, el. 4500 ft., *D. Axelrod 509* (UC–VTM); Cactus Flat, Cushenbury Grade, el. 6000 ft., *P. A. Munz 10502* (P, UC); 5 mi. w. of Warrens Well, *Ralph Hoffman* (SM 11743); granite ridge 2 mi. s. of the windmill, on Old Woman Well and Twenty-nine Palms Road, *Roxana Ferris & Ruth P. Rossbach 9508* (G, UC); crevice in granite, e. of Quail Spring, Joshua Tree National Monument, *Reid Moran 845* (D); crevices of granite rock and at foot of cliff by junction of main highway and Quail Spring road, *Mary Bowerman 4173* (UC); among rocks 1 mi. n. of Barker Dam, el. 4300 ft., Joshua Tree National Monument, *Annie M. Alexander & Louise Kellogg 2121* (G, UC). Riverside Co.: north base of San Jacinto Mts., Snow Creek Canyon, 1 mi. above fish hatchery,

FIG. 19. *Diplacus calycinus* Eastwood.

el. 2600 ft., *C. B. Wolf 3657* (D, R) ("flowers pale, creamy yellow, plant with 4 ft. spread and 2 ft. high"); rocky places near Pipe Creek, above Hemet Valley, San Jacinto Mts., el. 5500 ft., *C. B. Wolf 1960* (UC); exposed slope in vicinity of Chalk Hill, el. 4600 ft., San Jacinto Mts., *H. M. Hall 2077* (UC); Suicide Rock Trail above Idyllwild, el. 6300 ft., *M. Van Rensselaer 1922* (UC); rock crevices, 10 mi. sw. of Coahuila, *P. A. Munz 10884* (G, P); 1 mi. n. of San Diego Co. line, near Aguanga on Highway 71, *H. E. McMinn 5589, 5590* (UC). San Diego Co.: Warners Springs, *Mrs. A. L. Combs* (CA 28377); transplant in garden of F. F. Gander, from Montezuma Valley, between Warner Stage Station and Borego region, collected July 8, 1945, *H. E. McMinn & M. Van Rensselaer 1901* (UC) (appears to have some *D. aridus* genes); Borego Palm Canyon, *F. F. Gander 1284* (SD); stream below Eagles Nest Dam, Hot Springs Mt., *F. F. Gander 8746* (SD). San Luis Obispo Co.: in chaparral on e. slope of Pozo Range, 6 mi. s. of La Panza, el. about 2200 ft., *D. D. Keck 2827* (D, P, UC); about 1 mi. e. of Pozo Mt. summit, el. 2100 ft., *H. E. McMinn 5550* (UC); also along McGinnis Creek on road bank to within 6 mi. of La Panza; ½ mi. se. of mouth of Placer Creek, La Panza Quad., el. 1650 ft., *W. A. Peterson 828* (UC–VTM); 1.4 mi. se. of Avenales Ranch, Branch Mt. Quad. Sec. 29, T 31S, R 17E, el. 1850 ft., *T. M. Hendrix 1004* (UC–VTM).

Type. South Fork Kaweah River, 5800 feet altitude, Tulare County, California, July 22, 1904, *Culbertson 4407* (CA; isotypes G, P, NY, MO, UC, CA). All specimens of the type collection are similar in having more ovate to oval leaves than most specimens found growing at lower elevations. The specimens also are very densely woolly on upper stems, branches, lower surfaces of the leaves, on the calyces, and pedicels. According to Alice Eastwood (Bot. Gaz. 41: 287–288) it was first collected by T. S. Brandegee in the Kaweah Canyon, Tulare County, California, July 26, 1892.

References. *Diplacus calycinus* Eastw., Bot. Gaz. 41: 287 (1906); ex. C. F. Baker, West Am. Plants 3: 5 (1904), name only.

Mimulus longiflorus var. *calycinus* (Eastw.) Grant, Ann. Mo. Bot. Gard. 11: 331 (1924).

Diplacus longiflorus var. *calycinus* (Eastw.) Jepson, Man. 919 (1925).

9. Diplacus longiflorus Nutt. Southern Diplacus.

Figs. 20, 25-5.

An erect profusely branched shrub, 1 to 4 feet high, with the upper stems, branches, under surface of leaves, pedicels, and calyces densely pubescent and glandular-hairy to only slightly pubescent. Leaves 1 to 3½ inches long, ¼ to ¾ inch wide, lanceolate to linear-lanceolate or oblong, the upper surface yellowish to dark green, nearly glabrous, glandular, impressed-veiny, the lower surface densely covered with branched and simple glandular hairs, the margin finely toothed to nearly entire at base, often revolute, the axils frequently with short branchlets bearing several smaller and linear leaves. Pedicels ⅛ to ¼ or rarely ⅜ inch long, glandular-hairy; calyx 1 to 1½ inches long, the tube gradually expanding upward to a slightly more expanded throat which becomes somewhat contracted toward apex, covered with simple and branched non-glandular hairs and shorter glandular hairs; corolla typically orange-yellow, but varying from deep orange through light orange and buff to nearly white, 2 to 2½ inches long, the tube usually included, ½ to ¾ inch long, expanding gradually or abruptly into a funnel-shaped throat about ¾ inch long, the inner lower surface with 2 deep orange bands

separated by a single white band, the limb with a dorso-ventral spread of 1¼ to 1¾ inches and a lateral spread of the 3 lower lobes of 1⅛ to 1½ inches, the upper 2 lobes with a deep lateral

Fig. 20. *Diplacus longiflorus* Nutt.

notch and finely and irregularly toothed, extending at right angles or slightly recurved from the throat, the 3 lower lobes finely and irregularly 3- to 7-toothed to nearly entire or with 1 or 2 deeper notches, extending forward from the throat; stamens included; style with stigma included. Capsule about ¾ inch long, splitting along the upper suture. Flowering period, March to July.

Distribution. Southern Diplacus, in its typical form, is known from coastal southern California, where it occurs in the Pozo Mountains of San Luis Obispo County southward in scattered locations on the coastal drainage slopes of the mountains of Santa Barbara, Ventura, Los Angeles, and Orange counties. It also occurs on Santa Cruz and Santa Rosa islands, in a few locations in Lower California, in north central San Diego County, in the San Jacinto Mountains of Riverside County, and north and east of Bakersfield in Kern County.

Representative localities and specimens. Lower California, Mexico. All Saints Bay, April 16, 1885, *E. L. Greene* (D, UC–193606, G) [isotype of *D. arachnoideus* Greene, Bull. Calif. Acad. 1 (4): 210 (1885)]; bluff s. of La Mission, *A. G. Vestal & F. F. Gander 6017* (SD). California. San Diego Co.: Observatory Road, Palomar Mt., *F. F. Gander 6295* (SD). Riverside Co.: Idyllwild Grade, el. 3500 ft., *C. V. Meyer 211* (UC) (approaches *D. calycinus*); Reche Canyon, el. 1500 ft., *H. M. Hall* (UC 64230) (approaches *D. calycinus*); along Indian Canyon Truck Trail, Santa Ana Mts., el. 2100 ft., *H. E. McMinn & M. Van Rensselaer 1889 A–F* (UC) (series showing variation in flower color and in amounts of pubescence on the calyces and upper branchlets; some genes of *D. australis* and *D. puniceus* may be in these specimens); 8 mi. nw. of Elisnore, el. ca. 1500 ft., *C. L. Hitchcock 6044* (NY). Orange Co.: Trabuco Peak, Santa Ana Mts., el. 4000 ft., *W. Pequegnat* (P 256713); Santa Ana Canyon, near Rancho Santa Ana Bot. Gard., *H. E. McMinn & M. Van Rensselaer 1912* (UC) (approaches *D. australis*). Los Angeles Co.: Turnbull Canyon, near Whittier, *H. E. McMinn 1235* (UC), and *H. E. McMinn & M. Van Rensselaer 1913D, 1914C* (UC); San Dimas, *H. P. Chandler* (UC 26709); foothills, San Gabriel Mts., e. of La Crescenta, at junction of Oceanview Blvd. and Foothill Blvd., *H. E. McMinn 5600* (UC); canyon at Santa Monica, *J. B. Davy 2731* (UC); Mandeville Canyon, el. ca. 1100 ft., *I. Clokey 4441* (UC–Cl) (calyces only slightly hairy); Mt. Wilson, *Alice Eastwood 9033* (CA); San Fernando wash, *Alice Eastwood 3130* (NY). Ventura Co.: boulder-covered slope ca. 3 mi. e. of town of Santa Susana, *H. E. McMinn & M. Van Rensselaer 1886 E, F* (UC); ca. 8 mi. above Piru, along Piru Creek, *C. B. Wolf 2010* (D, UC) (calyx only slightly hairy); Mt. Pinos region, Goodenough Meadow bank, *W. R. Dudley & F. H. Lamb 4756* (D); Upper Ojai Valley, in openings in chaparral, *M. Van Rensselaer 1881, 1882* (UC); 1¾ mi. s. of Blue Point on Piru Creek, Tejon Quad. Sec. 22. T 5N, R 18W, *A. Simontacchi 81* (UC–VTM); Casitas Pass, el. 500 ft., *H. M. Hall 3160* (CM, UC). Santa Barbara Co.: on roadfill along Casitas Pass Road, ca. 3 to 4 mi. e. of Carpenteria, just off Highway 101, *H. E. McMinn & M. Van Rensselaer 1884, 1885* (UC); La Cumbre Trail in Mission Canyon, el. 2360 ft., *Clifton Smith 1409* (UC) (fls. orange-yellow), *1408* (UC) (fls. nearly white); Mission Canyon, *Alice Eastwood 19* (UC) (near type locality); near end of Gibraltar Lake, Santa Ynez Quad., el. 1700 ft., *W. A. Peterson 198* (UC–VTM); Cuyama River Canyon, el. 2000 ft., *Lyman Benson 5813* (P). San Luis Obispo Co.: ca. 9.8 mi. e. of Santa Margarita on road to Pozo, el. 1300 ft., *H. E. McMinn 5545* (UC) (fls. deep orange), *5546* (UC) (fls. light orange), *5547* (UC) (fls. nearly lemon-yellow); Calf Canyon, *Alice Eastwood & J. T. Howell 5912* (CA); Santa Margarita, Eldorado School, *Mary G. Wall* (CA 204605); 2½ mi. s. of Black Mt. Pozo Quad., Sec. 34, T29S, R15E, el. 1900 ft., *T. M. Hendrix 196* (UC–VTM) (approaches *D. calycinus*). Monterey Co.: near Camp 31, Guadalupe Ranch, May 11, 1861, *W. H. Brewer 586*, Geological Survey 1860–67 (UC). San Benito Co.: Rockhaven, 4 mi. e. Aromas, *Alice Eastwood & J .T. Howell* (CA 234442) (I visited this locality in 1947 and found only good *D. aurantiacus*). Kern Co.: 7 mi. n. of Bakersfield, M. Van Rensselaer seed lot 12, = *H. E. McMinn voucher 5603* (UC); Kern River Road, ca. 15 miles from Bakersfield, el. ca. 1500 ft., *F. W. Peirson 7309* (P); 1¾ mi. s. of Blue Point, Tejon Quad. Sec. 22, T5N, R18W,

FIG. 21. *Diplacus parviflorus* Greene.

el. 1200 ft., *A. Simontacchi 84* (UC–VTM). SANTA BARBARA CO. SANTA CRUZ ISLAND: Above Frey's Harbor, *H. E. McMinn 2790* (UC); also *H. M. Hall 8201* (UC, P); West Twin Canyon, el. 500 ft., *I. W. Clokey 5055* (UC, P); Dix Canyon, *I. W. Clokey 5056* (UC); Prisoner's Harbor, *I. W. Clokey 5054* (UC); Pelican Bay, *I. W. Clokey 5057* (K) (calyces hairy as in *D. calycinus*). SANTA ROSA ISLAND: *Helen E. Sweet* (P 214164) (flowers smaller than typical); *N. Dunn* (K).

Type. "Hab. Rocky places by small streams, in the vicinity of Santa Barbara." (Probably in Mission Canyon in 1836), Santa Barbara County, California, *Thomas Nuttall* (BM).

References. *Diplacus longiflorus* Nutt., Mss. (Oct. 12, 1837), Taylor's Ann. Nat. Hist. 1, no. 2: 139 (1838); Nutt., Curtis. Bot. Mag. new ser. 12: under plate 3655 (1838). Published as *Diplacus longiflora.*

Mimulus glutinosus var. *brachypus* Gray, Proc. Am. Acad. new ser. 8, whole ser. 11: 97 (1876), and in Bot. Calif. 1: 566 (1876).

Diplacus arachnoideus Greene, Bull. Calif. Acad. Sci. 1: 210 (1885) and 2: 409 (1887).

Diplacus speciosus Davy, Erythea 2: 101 (1894). This was described from a cultivated plant in the University of California Botanical Garden. The description and the type specimen (UC 26714) are matched by *D. longiflorus* Nutt., but the statement that the plants came from Humboldt County must be an error.

Mimulus longiflorus (Nutt.) Grant, in Gentes Herb. 1: 136 (1923), and in Ann. Mo. Bot. Gard. 11: 328 (1924).

10. Diplacus parviflorus Greene. Island Diplacus. Fig. 21.

A semi-erect or spreading subshrub, 6 inches to 2 feet or rarely to 4 feet high, with glabrous stems and leaves, the younger branches commonly reddish. Leaves 1 to 1¾ inches long, ⅜ to 1 inch wide, oval-elliptic, elliptic-lanceolate, or ovate to obovate, the upper surface dark green, glabrous, the lower surface paler, glabrous, glutinous, shining as though varnished, the margin entire or glandular-denticulate to finely and irregularly toothed, usually somewhat revolute, the axils often with a cluster of smaller leaves. Pedicels ⅜ to ¾ inch long, glabrous; calyx ¾ to 1 inch long, tubular, glabrous; corolla brick-red or orange-red, 1⅜ to 1¾ inches long, the tube included, ½ to ⅞ inch long, the throat narrowly funnelform, ¾ to ⅞ inch long, the limb with a dorsoventral spread of ¾ to ⅞ inch and a lateral spread of the 3 lower lobes of ⅝ to ¾ inch, the 2 upper lobes nearly entire or with a small lateral notch, spreading slightly forward from the throat, the 3 lower lobes narrow, entire or slightly toothed at their tips, extending forward from the throat; stamens included; style with stigma exserted. Capsule about ¾ inch long, opening along the upper suture. Flowering period, March to July, or nearly throughout the year.

Distribution. Island Diplacus is known only from Santa Rosa, Santa Cruz, Anacapa, and San Clemente islands, all off the coast of southern California. It occurs on shady hillsides and in dry canyons, usually near the shore.

Representative localities and specimens. California. Los Angeles Co. San Clemente Is.: wall of canyon s. of Lemon Tank on ne. side of island, *P. A. Munz 6707* (P); dry canyon and steep cliffs, near the sea on e. side, *Nell Murburger 33* (UC). Ventura Co. Anacapa Is.: slopes near bottom of gully below grove of *Quercus tomentella*, *Reid Moran 718* (D); canyon sides, *Ralph Hoffman* (SM) *5517*. Santa Barbara Co. Santa Cruz Is.: Above Frey's Harbor, *H. E. McMinn 2789* (UC); vicinity of Pelican Bay, *L. R. Abrams & I. L. Wiggins 32* (UC); between Orizaba Canyon and Baby's Cove, el. 200 ft., *C. B. Wolf 2902* (D). Santa Rosa Is.: slope above ranch house, *H. E. McMinn*

2746 (UC); shady hillside near Torrey Pine grove, *Reid Moran 811* (D); canyon near Black Mt., *John Voss* (P 171442).

Type. North side of Santa Cruz Island, Santa Barbara County, California, July and August, 1886, *E. L. Greene* (isotype, NY).

References. *Diplacus parviflorus* Greene, Pittonia 1: 36 (1887).

Mimulus parviflorus (Greene) Grant, Ann. Mo. Bot. Gard. 11: 344 (1924). Not *Mimulus parviflorus* Lindl., Bot. Reg. pl. 874 (1825).

Mimulus Flemingii Munz, Man. S. Calif. Bot. 477 (1935).

11. Diplacus puniceus Nutt. Mission Red Diplacus. Scarlet-flowered Diplacus. Fig. 22.

An erect and freely branched shrub, 1½ to 5 feet high, with glabrous usually reddish branches and glabrous or puberulent glutinous herbage. Leaves 1 to 3 inches long, ⅛ to ½ inch wide, linear-lanceolate to elliptic, the upper surface dark green, glabrous, the lower surface paler, glabrous to finely pubescent, glandular, the margin entire or finely toothed, usually revolute. Pedicel ½ to 1¼ inches long, glabrous; calyx ¾ to 1⅛ inches long, tubular, usually reddish; corolla brick-red or orange-red, 1¼ to 1¾ inches long, the tube included, ⅜ to ⅝ inch long, yellow, the throat narrow-funnelform, ½ to ¾ inch long, the limb with a dorso-ventral spread of 1 to 1¼ inches and a lateral spread of the 3 lateral lobes of ⅞ to 1 inch, the upper 2 lobes with a pronounced lateral notch and finely and irregularly toothed, spreading at right angles to the throat, the 3 lower lobes nearly entire to finely and irregularly toothed at the tips, slightly curving forward from the throat; stamens included or the anthers of the longer pair slightly exserted; style with stigma slightly exserted. Capsule ½ to ¾ inch long, splitting along the upper suture. Flowering period, March to July.

Distribution. Mission Red Diplacus is restricted to southern California and adjacent Mexico. Its typical form with glabrous herbage and long pedicels occurs mainly in the western portion of San Diego County, in a few localities in northern Lower California, and in Orange and western Riverside counties. On Santa Catalina Island it appears in less typical form with shorter pedicels and with more orange in the flowers. In several localities of west central Riverside County, Mission Red Diplacus shows the effect of gene contamination from *Diplacus longiflorus,* thus becoming somewhat pubescent and with shorter pedicels. It usually inhabits dry canyon slopes, mesas, lower mountain slopes, and fire-burns in the chaparral.

Representative localities and specimens. Lower California, Mexico. Granitic soil on foothills of Sierra San Pedro Martir in vicinity of Rancho San Jose, 25 mi. e. of San Telmo, el. 2600 ft., *Ada Meling 28* (D, P, UC); Pine Canyon, 6 mi. s. of San Vicente, *C. Epling & Wm. Stewart* (D 254531); n. of Ensenada, on chaparral-covered hillside 3.8 mi. ne. of Sauzal along road to Guadalupe, *I. L. Wiggins 10067* (D). California. San Diego Co.: Otay Mt., *F. F. Gander 223.73* (SD); Barrett Dam Road, 5–6 mi. from Jamul, *I. L. Wiggins 1950* (UC); s. side of Mission Canyon, between Old Town and San Diego Mission, *H. E. McMinn & M. Van Rensselaer 1907 & 1908* (UC); Mt.

FIG. 22. *Diplacus puniceus* Nutt.

Helix, *H. E. McMinn 5591* (UC); La Jolla, in canyon near Scripps Biol. Inst., *H. E. McMinn 1415* (D); Mussey Grade, between Lakeside and Ramona, *G. R. Fleming & W. W. Eggleston 19645* (P); first-year fire-burn in chaparral, Poway Grade, *F. F. Gander 770* (SD); Ramona, *F. F. Gander 684* (SD); hills near Ysidora, *L. R. Abrams 3285* (MO, NY); Pala Grade, Temecula to Pala, *H. L. Mason 3119* (UC); Herron Ranch near De Luz, *F. F. Gander 8266* (SD); upper San Onofre Canyon, *F. F. Gander 8419* (SD). Orange Co.: Hot Springs, San Juan Canyon, el. 1200 ft., *R. St. John 205* (UC–VTM); Laguna Canyon, ca. 5 mi. e. of Laguna Beach, *H. E. McMinn & M. Van Rennselaer 1911* (UC) (in series of *D. puniceus* × *D. australis*); Sierra Canyon, Santa Ana Mts., el. 1200 ft., *P. A. Munz & R. D. Harwood 3758* (D, P, UC). Riverside Co.: near summit of Temecula—Rainbow Grade, *H. E. McMinn & M. Van Rensselaer 1900 A, C* (UC); s. of Elsinore, *H. E. McMinn 3939* (UC) (pedicels shorter); steep decomposed granite slope along Indian Canyon Truck Trail, e. side Santa Ana Mts., el. 2600 ft., *H. E. McMinn & M. Van Rensselaer 1890 A, B, C, 1891* (UC); Butte w. of Lakeview, *I. M. Johnston 2286 & 2298* (MO, P) (close to *D. puniceus* but for pedicel length, these belong to a hybrid swarm of *D. puniceus* × *D. australis* × *D. longiflorus*). Los Angeles Co. Santa Catalina Is.: (Most specimens have some genes of *D. australis* in them). Avalon, rocky banks along shore, *I. J. Condit* (UC 455548); Pebbly Beach Road, el. 50 ft., *F. M. Reed 2816* (UC); Avalon Canyon, above last almond orchard, *C. B. Wolf 3509* (UC) ("Trunk dia. 1 inch, ht. 4 ft., spread 4 ft., corollas deep red-brown outside").

Type. ". . . in sandy loam by the borders of small winter streams," near San Diego, San Diego County, California, *Thomas Nuttall* (BM).

References. *Diplacus puniceus* Nutt., Mss. (Oct. 12, 1837), Taylor's Ann. Nat. Hist. 1, no. 2: 137 (April 1838); Curtis Bot. Mag. new ser. 12: colored plate 3655, opposite page of description (May 1, 1838). "It was discovered by Nuttall, and transported in 1836 to the garden of Mr. Buist, the extensive nurseryman of Philadelphia, by whom the whole stock was sent, in the autumn of last year, to Messrs. Lowe, of Clapton, who are consequently the only possessors of it." Published as *Diplacus punicea.*

Mimulus puniceus (Nutt.) Steud., Nom. Bot. ed. 2, pt. 2, 150 (1841). Name only; Gray, Syn. Fl. N. Am. ed. 2, 21, Suppl. 442 (1886).

Diplacus glutinosus var. *puniceus* Benth., DC. Prodr. 10: 368 (1846); Lindl. Paxt. Fl. Gard. 8: 95 (1852–1853).

Mimulus glutinosus var. *puniceus* Gray, Bot. Calif. 1: 566 (1876).

12. **Diplacus rutilus** (Grant) comb. nov. Red Diplacus. Fig. 23.

An erect freely branching shrub, 1½ to 3 feet high, with more or less densely pubescent and glandular-hairy stems, branches, lower surfaces of leaves, calyces, and pedicels. Leaves 1½ to 3 inches long, ⅜ to ¾ inch wide, linear-lanceolate to broadly oblong-lanceolate, the upper surface dark green, glabrous, or with a few glandular hairs, distinctly impressed-veiny, the lower surface lighter green, obviously villous with numerous long simple and fewer branched glandular hairs, the margin finely toothed to nearly entire, revolute, the axils often with a cluster of several smaller linear leaves. Pedicel ⅛ to ¼ inch long, glandular-hairy; calyx 1¼ to 1½ inches long, glandular-hairy, usually tinged with red, the basal tubular portion expanding gradually to abruptly upward into a broader throat which is somewhat contracted near apex; corolla deep velvety red, the edges of the lobes often tinged with yellow, 1¾ to 2½ inches long, the in-

cluded tube 3/4 to 7/8 inch long, yellow, the throat abruptly expanded from the tube, 3/4 to 7/8 inch long, the limb with a dorsoventral spread of 1 5/8 to 2 inches and a lateral spread of the 3 lower lobes of 1 3/8 to 1 5/8 inches, the 2 upper lobes with a pronounced lateral notch and irregularly toothed, spreading at right angles to the throat or slightly recurved, the 3 lower lobes irregularly and finely to coarsely toothed or rarely nearly entire at their tips, curving forward from the throat; stamens included; style with stigma included. Capsule about 3/4 inch long, opening along the upper suture. Flowering period, March to June.

Distribution. Red Diplacus occurs in coastal southern California in a few scattered localities in southeastern Ventura, Los Angeles, and western Riverside counties. It is associated with *Diplacus longiflorus* and with hybrids between these two.

Representative localities and specimens. California. Ventura Co.: boulder-covered slopes about 3 mi. e. of Santa Susana, *H. E. McMinn & M. Van Rensselaer,* in series *1886 A–F* (UC); Santa Susana Pass, *Adele L. Grant 1650* (D, K, G, P). Los Angeles Co.: hills near Chatsworth Park, *F. Grinnell, Jr.* (P 8128); near San Dimas Canyon, *P. A. Munz 3362* (MO, P); hills w. of Pomona on Highway 99, near summit, *H. E. McMinn & M. Van Rensselaer 1888 A* (UC) (flowers smaller and calyces less hairy than in some specimens); Turnbull Canyon, near Whittier, *H. E. McMinn & M. Van Rensselaer 1913 A* (UC); San Dimas Canyon Park, Pomona Quad. Sec. 36, T 1H, R, 9W, el. 1200 ft., *Jerome S. Horton 338* (UC–VTM); base of Santa Susana Pass, el. 1200 ft., abundant in sandstone, *C. B. Wolf 7772* (UC); Chatsworth Lake, *J. F. Ashley* (UC 688888). Riverside Co.: along Indian Canyon Truck Trail, Santa Ana Mts., el. 2800 ft., *H. E. McMinn & M. Van Rensselaer 1894 A* (UC) (probably some genes from *D. australis* and *D. puniceus* in this).

Type. Rocky outcropping at Santa Susana Pass, Ventura County, California, June 10, 1920, *Adele L. Grant 1650* (MO 894182).

References. *Diplacus rutilus* (Grant) McMinn.

Mimulus longiflorus var. *rutilus* Grant, Ann. Mo. Bot. Gard. 11: 333 (1924).

Diplacus longiflorus var. *rutilus* (Grant) McMinn, Ill. Man. Calif. Shrubs 498 (1939).

13. Diplacus stellatus Kell. Cedros Island Diplacus.

This taxon is of uncertain status. It is known to me only from herbarium specimens collected on Cedros Island, Mexico. From these specimens, it is not possible to discern the color of the flowers. E. L. Greene, however, reported the flowers to be the same color as those of *D. aurantiacus* (*D. glutinosus*), namely orange-yellow, and only half as large.

Original Description. "Stem shrubby, erect, striate, stellate, hoary, dry. Leaves lanceolate, narrowed at the base and apex, quite entire; margins revolute, clammy, varnished, green above, dry, densely stellate and hoary beneath; apex terminated by a large gland. Peduncles short, axillary, solitary (about half the length of the calyx, or one-fourth that of the leaves). Calyx tubular, elongated (three-fourths to one inch in length), five-angled, angles slightly winged, teeth unequal, two upper longest. Flowers small, tube long (one inch or more), somewhat arched. Stem light cinnamon or orange color."

FIG. 23. *Diplacus rutilus* (Grant) McMinn. (*Mimulus longiflorus* var. *rutilus* Grant.)

The name *stellatus* is a misnomer, for the stellate hairs certainly do not belong to this species or any other species in the genus *Diplacus*. The under surfaces of the leaves are densely covered with simple and branched glandular and non-glandular hairs. Numerous stellate hairs undoubtedly from other plants have apparently been caught by the glutinous foliage, and are found scattered over the specimens examined.

Specimens examined. Lower California, Mexico. Cedros Island: *Dr. J. A. Veatch* (G), without date; *E. L. Greene,* May 1, 1885, in fruit (D 77466, MO 92468); *E. L. Greene,* April 30, 1885, in flower (BM); *Dr. Edward Palmer 728,* March 18–20, 1889 (G) (flowers small, resemble those of *D. parviflorus*); *A. W. Anthony 47,* July–October 1896 (D, G, UC) (leaves revolute, densely glandular-hairy beneath, glandular and glutinous above, the pedicels and younger upper branchlets minutely glandular-hairy, flowers small, the corolla-tube somewhat arched as in *D. parviflorus*); *T. S. Brandegee,* April 1, 1897, in flower (MO) (leaves ¾ to 1¼ inches long, ovate-lanceolate or lanceolate to linear-lanceolate, distinctly glandular and golden-pubescent beneath, glabrous and glutinous above, revolute; pedicels about ¼ inch long; calyx glabrous or nearly so).

Type collection. Cedros Island, Baja California, Mexico, without date, *Dr. John A. Veatch* (G).

References. *Diplacus stellatus* Kell., Proc. Calif. Acad. ser. I, 2: 18 (1863). *Diplacus glutinosus* var. *stellatus* (Kell.) Greene, Pittonia 2: 155 (1890). *Mimulus stellatus* (Kell.) Grant, Ann. Mo. Bot. Gard. 11: 337 (1924).

14. **Diplacus linearis** (Benth.) comb. nov. Fig. 24.

This entity is discussed under section treating natural hybrids (p. 87).

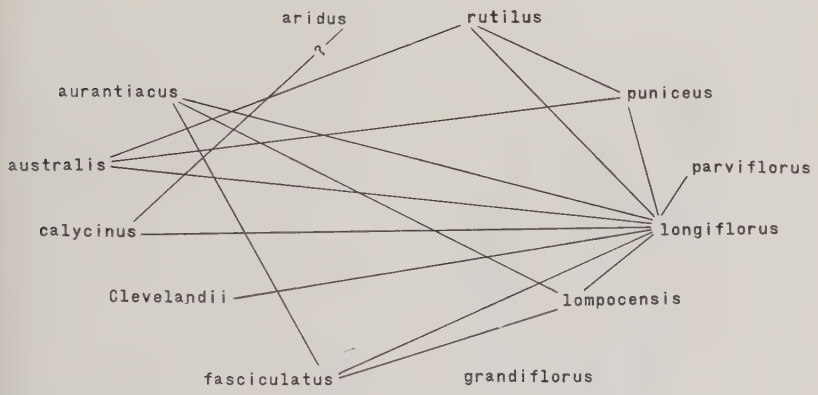
Type. Nova California, 1833, *D. Douglas* (BM).

References. ×*Diplacus linearis* (Benth.) McMinn. *Mimulus linearis* Benth., Scroph. Ind. 27 (1835).

Hybrids

The variations that exist in a population of plants are always of interest to the taxonomist. To discover the nature of these variations is one of the main functions of taxonomic botany. Are they due to gene mutations which may be the starting points for new subspecies or species? Are they due to the action of local environmental factors and therefore considered as modifications which are of little consequence in starting new fixed entities? Or are they due to hybridization of two or more interfertile entities which overlap in their geographical distribution? In an effort to answer these questions for the genus *Diplacus,* I have studied many populations in the field and in the garden, and have made numerous crosses involving most of the natural entities. Evidence obtained from these populations and crosses convinces me that most of the variations are due to natural hybridization of two or more field entities which in the past occupied, or which now occupy, areas of overlapping distribution. I also believe that hybridization, particularly the introgressive type, has been important in the evolution of this genus. Some of the observa-

TABLE 1. DIAGRAMMATIC REPRESENTATION OF NATURAL CROSSES OCCURRING AMONG THIRTEEN FIELD ENTITIES



tions supporting these conclusions are presented under the three following subheadings: Natural Hybrids, Artificial Hybrids, and Garden Hybrids. Natural hybrids may be referred to as field hybrids. They include all hybrids which occur naturally in the wild. Artificial hybrids are those resulting from hand-pollination. Garden hybrids include those which occur without hand-pollination when different entities are brought into cultivation.

Natural Hybrids. In the following discussion of a few of the known field hybrids and hybrid swarms or populations, I shall begin with those that occur farthest to the north and probably the farthest away from the assumed point of origin and center of distribution of the genus. The natural field crosses are graphically represented in table 1. For a clear understanding of these hybrids, it is necessary that the studies be made upon living plants because herbarium material is not reliable for determining the color and the size of flowers.

From observations made upon field hybrids, it appears that when the putative parents occupy the same area as the hybrids, the population shows a wide range of variation, while if only one parent is present, the putative hybrids more closely resemble that parent, and if neither parent now occupies the area populated by the putative hybrids, the latter tend to be much more uniform and often intermediate, in many characters, between the two putative parents.

D. aurantiacus × *D. fasciculatus* [× *D. linearis* (Benth.) McMinn], fig. 24. Hybrid populations which display innumerable

variations between *D. aurantiacus* and *D. fasciculatus* have been observed in the Upper Carmel Valley, along the Big Sur River in Monterey County, and along Chalone Creek and its washes in the Pinnacles National Monument in San Benito County. Some of

Fig. 24. Type of × *Diplacus linearis* (Benth.) McMinn. (*Mimulus linearis* Benth.) Specimen at the British Museum of Natural History.

the specimens in the Chalone Creek area are slightly pubescent, a condition which may be due to an infiltration of genes from *D. longiflorus,* a third field entity which has been collected in a few scattered localities in adjacent Monterey and San Luis Obispo counties.

In the region of the headwaters of the Big Sur River in the Santa Lucia Mountains of Monterey County, *D. fasciculatus* occurs in typical form, while at the lower reaches of the river most specimens which appear as that entity possess characters undoubtedly the result of genes from *D. aurantiacus,* the common entity at the mouth of the Big Sur River and adjacent coastal bluffs. Garden plants grown from seeds of these putative hybrids display the same variations as found in the natural populations.

In September, 1945, Mrs. Hans Ewoldsen sent the writer seeds which she had collected at Big Sur, California, from a population of *Diplacus* which appeared to possess characters of *D. fasciculatus* and *D. aurantiacus*. Seven lots of seeds, each lot collected from a different plant, were planted in the trial garden. Of the numerous plants grown from these seeds, only a few showed a combination of characters sufficient to classify them either as *D. aurantiacus* or *D. fasciculatus*. Most of the plants displayed recombinations of characters which had probably resulted from gene flow between the putative parents, *D. aurantiacus* and *D. fasciculatus*, and the progeny of their subsequent backcrosses and intercrosses (introgressive hydridization). Five plants from each of the seven lots were chosen at random for further observation under as nearly uniform conditions as the garden normally provided. Plants of lot 6A displayed foliage characteristics more like those of *D. aurantiacus*. Plants of lot 6B showed more variation in foliage characters, but none had the pubescence on the lower leaf-surfaces which is characteristic of most leaves of *D. aurantiacus*. One plant had leaves quite similar to those of *D. grandiflorus*, an entity closely related to *D. fasciculatus* which is found in the northern Sierra Nevada. The plants of lots 6C and 6E possessed foliage characters much like those of *D. fasciculatus*, while those of lots 6D, 6F, and 6G had intermediate foliage characteristics. Only a few plants had flowers with the deep corolla-lobe notches characteristic of *D. fasciculatus*.

The type specimen of *Mimulus linearis* Benth. (fig. 24) collected by David Douglas "in California" so closely matches one of these hybrids that I have concluded that Douglas must have collected his specimen from one of the hybrid populations, and that it should be recognized as × *Diplacus linearis* (Benth.) McMinn.

Representative specimens and localities. California. San Benito Co.: Pinnacles National Monument, entrance to camp grounds, *H. E. McMinn 5471–5476* (UC); wash into Chalone Creek, *H. E. McMinn 5534* (UC). Monterey Co.: upper Carmel River Valley, with *D. fasciculatus, H. E. McMinn 5519* (UC); near Big Sur P. O., *H. E. McMinn & Mrs. Hans Ewoldsen 5481–5484* (UC); about 19 miles from King City, along road through Hunter Liggett Military Reservation to Memorial Park, el. 1250 ft., *H. E. McMinn 5541* (UC); Santa Lucia Mts., *R. A. Plasket 122* (G, NY). San Luis Obispo Co.: 7.3 mi. w. of Paso Robles, on Adelaida Road, el. 1620 ft., *H. E. McMinn 5553* (UC); 6 mi. s. sw. of Lynch Ranch, Bradley Quad. Sec. 10, T 25S, R 9E, el. 1800 ft., *K. E. Bradshaw 171* (UC–VTM); 1.9 mi. e. ne. of Lincoln School, Adelaida Quad. Sec. 18, T 26S, R 11E, el. 1100 ft., *G. T. Nordstrom 1131* (UC–VTM). There may be some *D. longiflorus* genes in the San Luis Obispo County material.

D. aurantiacus × *D. longiflorus* (× *D. fasciculatus?*). Along the road banks on the Jolon Grade southwest of King City a population occurs in which most of the plants have considerable pubescence on the calyces, the upper branchlets, and lower surfaces of the leaves and in which the flowers are of a yellow hue varying in intensity and value. This hybrid population could be the result

of crossing and backcrossing between *D. aurantiacus* and *D. longiflorus,* and probably *D. fasciculatus* is also involved. These three natural entities, although not now occuring in pure form at that locality, do occur in the general area.

Farther south in Monterey and San Luis Obispo counties and in northwestern Santa Barbara County it is difficult to assign most of the plants observed at the lower elevations to any of the typical forms of the currently described field entities. They appear, in some localities, to be intermediate between *D. aurantiacus* and *D. facsiculatus,* in other localities, between *D. longiflorus* and *D. fasciculatus,* and in still others, between *D. aurantiacus* and *D. longiflorus.* These intermediate variants appear rather uniform in many characteristics and may represent a segregating population which possesses an entirely new combination of genes better suited to the areas in which they occur than were the putative parents. Most of these areas, although they now appear rather stable, show evidence of having been disturbed at some earlier time. This is particularly noticeable in populations on and adjacent to Lompoc Mesa in Santa Barbara County. These rather uniform populations appear as nearly glabrous forms of the light orange-colored *D. longiflorus* and are herein considered under the binomial *D. lompocensis.* Occasional specimens have been observed throughout the distributional area of *D. longiflorus* which are nearly as glabrous as the plants on Lompoc Mesa. In many characteristics these plants are quite similar to those from west central San Diego County which have been referred to *D. australis.* However, the hairy lower surfaces of the upper leaves, the minutely pubescent upper branchlets, and larger calyces of the Lompoc plants set them apart from the San Diego entity.

Representative specimens and localities. California. Monterey Co.: Jolon Grade, el. 1400 ft., 12 m. sw. of King City, *H. E. McMinn 5535-5540* (UC), also *L. R. Abrams 6467* (D, NY) ("flowers orange color"); *6469* (D, NY) ("flowers cream-yellow"); *6470* (D, NY) ("flowers pale cream color"). San Benito Co.: along Tres Piños Creek, 1 mi. se. of Emmet School, Panoche Pass Road, *I. L. Wiggins & Roxana Ferris 9354* (D); wash into Chalone Creek, Pinnacles National Monument, *H. E. McMinn 5532, 5533* (UC). San Luis Obispo Co.: 10 mi. w. of Paso Robles, on Adelaida Road, el. 1700 ft., *H. E. McMinn 5554* (UC); 13 mi. w. of Paso Robles, *Roxana Ferris 9767* (D); ½ mi. se. of mouth of Placer Creek, el. 1650 ft., La Panza Quad., *W. A. Peterson 828* (UC–VTM).

D. lompocensis × *D. longiflorus* × *D.?* Some specimens growing in areas adjacent to the Lompoc Mesa area of Santa Barbara County show the effect of gene flow from *D. lompocensis, D. longiflorus, D. aurantiacus* and probably *D. fasciculatus.*

Representative specimens and localities. California. Santa Barbara Co.: Gaviota Pass. *L. R. Abrams 5033* (D), and *Ralph Hoffman* (SM 11487); Zaca Lake, *Ralph Hoffman* (SM 9882); Madulce, San Rafael Mts., el. 5500 ft., *Ralph Hoffman* (SM 7590); brushy hillsides, Hope Ranch, *Ralph Hoffman* (SM 2787).

D. longiflorus × *D. parviflorus. Diplacus longiflorus* and *D.*

parviflorus are the only distinct entities found on Santa Cruz Island. The former usually inhabits the open hillsides and the latter occurs on the shady slopes and in canyons. In several places where these two taxa have invaded common ground, hybrid swarms are found displaying many combinations of leaf, calyx, and corolla characters.

Representative specimens and localities. Santa Barbara Co. Santa Cruz Island: "steep ravine above Marine Garden, el. ca. 600 ft.," *Ira W. Clokey 5059* (CM, P, UC) (calyx slightly villous, with shape of *D. parviflorus,* flowers reddish but much larger than in *D. parviflorus*); Frey's Harbor, el. 80 ft., *A. L. Grant 1704* (D, P) (corolla bronze to salmon color); Friar's Canyon, *Ira W. Clokey 5205, 5177* (UC–Cl) (from a hybrid swarm). Santa Cruz Island without specific locations: *Ralph Hoffman* (SM 11145, 1279, 2385) (flowers large, with varying shades of red and yellow, calyces large and small, glabrous to hairy); *H. M. Hall 8202* (UC), *L. R. Abrams & I. L. Wiggins 144, 135* (UC).

D. longiflorus × *D. rutilus.* In the Santa Susana Pass area of Ventura County, on the hills west of Pomona, in Turnbull Canyon near Whittier in Los Angeles County, and on the eastern slope of the Santa Ana Mountains of western Riverside County, many hybrids have been observed involving *D. longiflorus* and *D. rutilus.* These two entities are quite similar in all characteristics except for the color of their flowers. The former has orange-yellow flowers of varying intensity and value and the latter has dark red ones. Although varying most conspicuously in the color of their flowers, these hybrids show some variations in leaf and stem characters, in size, shape, and pubescence of calyces, and in the size of their flowers as well. These variations are probably due to the infiltration of genes from *D. puniceus* or its hybrids with those of *D. longiflorus* and *D. australis,* which entities may occur in the same areas. (See *D. longiflorus* × *D. rutilus* × *D. puniceus* × *D. australis*).

Representative specimens and localities. California. Ventura Co.: boulder-covered slope ca. 3 mi. e. of Santa Susana, *H. E. McMinn & M. Van Rensselaer 1886 B, C, D* (UC). Los Angeles Co.: hills w. of Pomona, summit of grade on Highway 99, *H. E. McMinn & M. Van Rensselaer 1888 B, C,* (UC); Turnbull Canyon, near Whittier, *H. E. McMinn & M. Van Rensselaer 1913 B, C* (UC). Riverside Co.: Indian Canyon Truck Trail, e. slope of Santa Ana Mts., el. 2100 ft., *H. E. McMinn & M. Van Rensselaer 1889 D, E, F,* (UC), probably some *D. puniceus* genes in these specimens.

D. longiflorus × *D. Clevelandii.* The only known occurrence of natural hybrids between *D. Clevelandii* and any other field entity is on the eastern flanks of the Santa Ana Mountains in western Riverside County. In this area *D. Clevelandii* normally occurs at elevations above 3000 feet and *D. longiflorus* at elevations below 3000 feet. Here at an elevation of 3150 feet along the Indian Canyon Truck Trail both of these entities were found as well as a number of apparent hybrids. Some of the hybrid plants were as much as three feet high and had the definite woody stems of *D. longiflorus,* while others resembled in habit of growth and in leaf characters the other putative parent, *D. Clevelandii.* One

FIG. 25. Young plants of *Diplacus*: *1*, *D. Clevelandii*; *5*, *D. longiflorus*; *2*, *3*, *4*, *6*, and *7*, hybrids of *D. longiflorus* × *D. Clevelandii*.

specimen (*1895B*) has pedicels 1 inch long. Such long pedicels may be due to genes from *D. puniceus,* which occurs at lower elevations down the trail. Plants grown from seeds of these hybrids show many characteristics intermediate between the assumed parents (fig. 25, -2-3-4-6-7). A differential survival value was distinctly exemplified by the garden-grown progeny. Those with a greater share of *D. longiflorus* characters thrived while those with presumably more genes from *D. Clevelandii* soon died under garden conditions.

This hybrid population was of interest, especially since *D. Clevelandii* differs in the character of fruit dehiscence from all other entities of the genus *Diplacus.* In its habit of growth and the configuration of the flowers, *D. Clevelandii* resembles some members of the genus *Mimulus* more than any of the entities in the genus *Diplacus.*

Representative specimens and localities. California. Riverside Co.: along Indian Canyon Truck Trail, east side Santa Ana Mts., el. 3150 ft., *H. E. McMinn & M. Van Rensselaer 1895, 1896* (UC).

D. calycinus × *D. aridus?* In the Warner's Hot Springs-Borego area of north central San Diego County there occur plants which appear to be very close to *D. calycinus,* but which show some characters of *D. aridus* as well. It may be that *D. calycinus* itself is of hybrid origin, the outcome, probably, of crosses involving *D. longiflorus* and *D. aridus.* See Artificial Hybrids p. 110 and Biological Relationships p. 117.

D. puniceus × *D. australis.* In many areas of San Diego County, in a few localities in adjacent Orange and Riverside counties, in northern Lower California, and on Santa Catalina Island, there are to be found hybrid swarms which have probably resulted from the crossing and backcrossing of *D. puniceus* and *D. australis.* In these swarms, introgressive hybridization has evidently been going on for so long that "yellow-flowered" *D. puniceus* and "red-flowered" *D. australis* plants are to be found.

On Santa Catalina Island most of the plants appear to represent polymorphous entities intermediate in character between *D. australis* and *D. puniceus.* The red-flowered, puniceus-like plants usually have the short pedicels characteristic of *D. australis.*

Representative specimens and localities. California. Orange Co.: north slope of Laguna Canyon, ca. 5 mi. e. of Laguna Beach, *H. E. McMinn & M. Van Rensselaer 1909 A–I, 1910, 1911* (UC); 2 mi. e. of San Juan Hot Springs, *Alice Eastwood & J. T. Howell 3931* (CA); Santiago Canyon, *H. M. Hall 9404, 9405* (UC). Riverside Co.: Smith Mt., *H. M. Hall* (UC 26710); Temecula Grade to Rainbow, *H. E. McMinn & M. Van Rensselaer 1900 A–D* (UC). San Diego Co.: head of Deluz Creek, el. 1000 ft., *H. A. Jensen 151* (UC–VTM), close to *D. puniceus;* Castro Canyon of Agua Tibia, *F. F. Gander 4315* (SD); top of rocky bluff between San Vicente Creek and San Diego River, near Lakeside, *F. F. Gander 1812* (SD); near county line on U. S. Highway 395, *F. F. Gander 3648* (SD); "hillsides", Ballena, Cleveland Collection 7004 (SD); burn at Dulzura, *F. F. Gander 9450* (SD); Bear Valley, Cleveland collection 1156 (SD); along highway to Palomar Mt., *Mrs. Ethel Higgins* 3(=*H. E. McMinn*

TABLE 2. POTENTIAL RECOMBINATIONS INVOLVING THREE SINGLE GENE CHARACTERS

Single Gene Characters			Combination number	Potential or Resulting Forms
Pedicel short (1/4 to 3/8 in.)	Calyx distinctly hairy	Flowers red	1	rutilus
		" intermed.	2	longiflorus x rutilus
		" yellow	3	longiflorus
	Calyx intermed.	" red	4	rutilus x puniceus x ?
		" intermed.	5	rutilus x australis
		" yellow	6	longiflorus x australis
	Calyx glabrous	" red	7	puniceus x australis
		" intermed.	8	australis x puniceus x ?
		" yellow	9	australis
Pedicel long (3/8 to 1 inch)	Calyx glabrous	" red	10	puniceus
		" intermed.	11	puniceus x australis
		" yellow	12	linearis x puniceus x ?
	Calyx intermed.	" red	13	puniceus x longiflorus x ?
		" intermed.	14	puniceus x longiflorus?
		" yellow	15	longiflorus x puniceus
	Calyx hairy	" red	16	puniceus x rutilus
		" intermed.	17	puniceus x longiflorus x ?
		" yellow	18	puniceus x longiflorus x ?

When only three characters are considered (length of pedicel, calyx surface, flower color), there are eighteen combinations which might result if single genes are presumed to recombine freely. Plants exemplifying 16 of these recombinations have been found in nature, the other two in garden culture.

5487) (UC); hills near Ysidora, *L. R. Abrams 3286* (G, P, NY). Los Angeles Co. Santa Catalina Island: Hamilton Canyon, near Avalon, *F. R. Fosberg S 4434* (P); Hamilton Beach, *F. R. Fosberg S 4497* (P, NY); canyon above Villa Park, *F. R. Fosberg 8121* (P); Pebbly Beach road, el. 50 ft., *F. M. Reed 2816* (UC); Big Wash, dry creek bed, *L. W. Nuttall 1008* (P).

D. longiflorus × *D. rutilus* × *D. puniceus* × *D. australis.* In several localities in southern California, hybrid swarms are found which appear to result from the crossing and the subsequent backcrossing of two or more of the following entities: *D. longiflorus, D. rutilus, D. puniceus,* and *D. australis.* Table 2 represents eighteen combinations which could be expected if single genes for the following characters were to recombine freely: length of pedicel, hairiness of calyces, and color of flowers. If other characters, such as size of flowers and hairiness of foliage, were considered, the chart could be extended to show innumerable combinations. All but two (Nos. 16, 17) of the eighteen possible combinations have been observed in field hybrid-swarms, and two of these (Nos. 16 and 17) have appeared in garden cultures. The total number of combinations would depend upon the degree of inbreeding and the number of pairs of factors involved.

In areas adjacent to large populations of *D. longiflorus,* the hybrids show a preponderance of *D. longiflorus* characters, but

where they are adjacent to large populations of *D. puniceus* or *D. australis,* they have more characters in common with these two latter entities.

Representative specimens and localities. California. Ventura Co.: Santa Susana Pass, *H. E. McMinn & M. Van Rensselaer 1886 A–F* (UC), *A. Grant 1650* (D, G, P) is *D. rutilus*; Goodenough Meadow, Mt. Pinos region, *W. R. Dudley & H. Lamb 4756* (UC). Los Angeles Co.: hills near Chatsworth Park, *F. Grinnell, Jr.,* (P 8128, 8131); San Antonio Canyon, Claremont, *C. F. Baker 5354* (UC, P); San Dimas hillsides, el. 2000 ft., *H. P. Chandler* (UC 27611), pedicels of *D. puniceus;* Turnbull Canyon, near Whittier, *H. E. McMinn & M. Van Rensselaer 1913 A–D, 1914 A–C* (UC); San Jose Hills w. of Pomona, *H. E. McMinn & M. Van Rensselaer 1888 A–D* (UC), *P. A. Munz & R. D. Harwood 3339, 3355, 3356* (P); Puddington Canyon, *Munz, Street, & Williams 2447* (P). See Catalina Island under Los Angeles Co., for *D. puniceus* × *D. australis.* Orange Co.: Santa Ana Mts., Bear Springs, el. 4300 ft., Trabuco Peak, el. 4000 ft., *W. Pequegnat* (P 256706, 256713); ca. 5 mi. e. of Laguna Beach, *H. E. McMinn & Van Rensselaer 1910 A–D, 1909 A–I, 1911 A–E* (UC). Riverside Co.: Indian Canyon Truck Trail, e. slope Santa Ana Mts., el. 2100-2800 ft., *H. E. McMinn & M. Van Rensselaer 1894 A–F, 1889 A–F, 1892, 1893,* (NC); Gavilan Hills, vicinity of Riverside, el. 500 ft., *H. M. Hall 2928* (CM, P, UC); butte due w. of Lakeview, *I. M. Johnston 2280–2298* (P), (P 8582); Pleasants Peak (Sugarloaf Pk.), el. 4000 ft., *W. Pequegnat* (P 256714); dry hills near Temecula, *P. A. Munz 2145* (P); Temecula Grade to Rainbow, near summit, *H. E. McMinn & M. Van Rensselaer 1900 A–D* (UC). San Diego Co.: San Felipe Creek, Chariot Canyon, *D. D. Keck & Alice McCully 115* (P); low chaparral near Mt. Helix, *I. L. Wiggins 1878* (P, UC), close to *D. puniceus* × *D. australis*; Bear Valley, *D. Cleveland* (SD 7003).

Artificial Hybrids. With the main objectives of obtaining more desirable plants for use as garden ornamentals and of determining the biological relationships between taxa in *Diplacus,* a program of artificial hybridization of field entities was initiated in the spring of 1946 and continued through 1949. This program was interrupted temporarily during 1950 because of the writer's absence abroad.

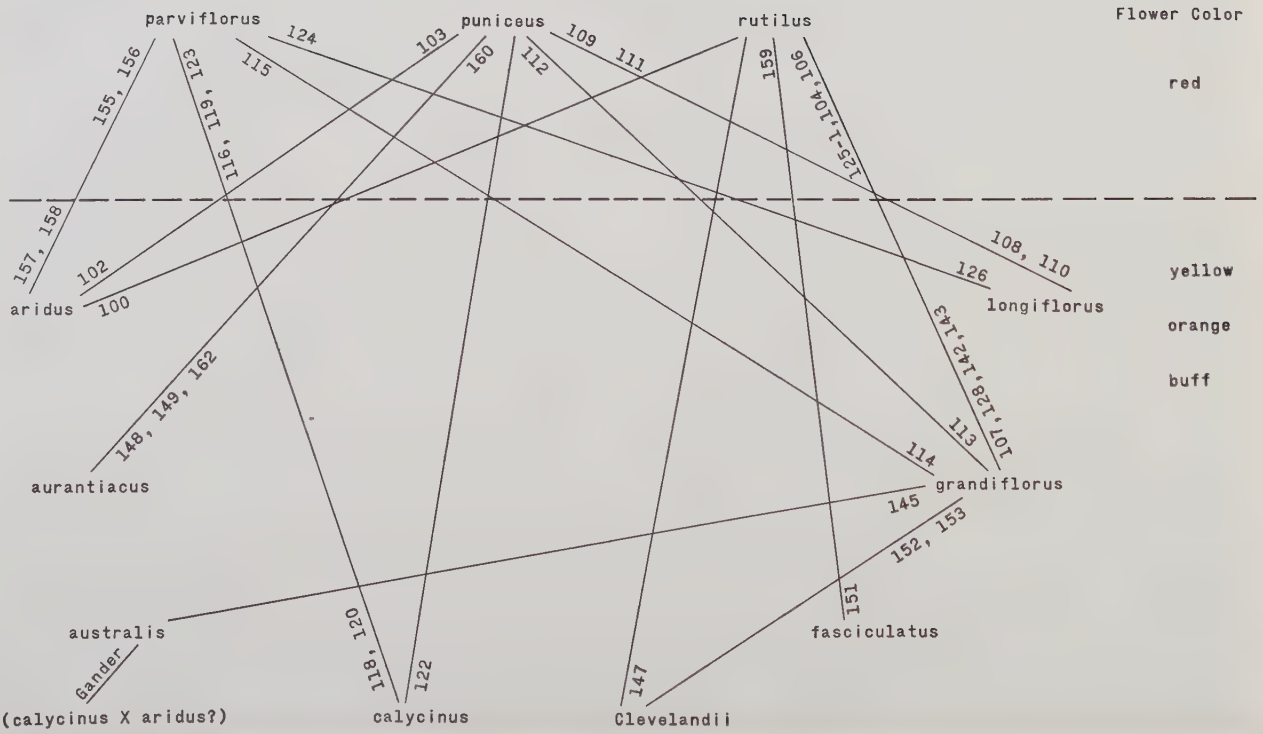
The parental plants for these experiments were mainly of two types: those grown from seed, and living plants transplanted from the field. In both cases, material was obtained in areas where there was little chance for contamination by another entity. In the cases of the parent plants of *D. parviflorus* and *D. rutilus,* which were garden-grown, it was necessary to "self" the plants to be certain of their constancy. Subsequent to the original crossings, plants from all parent populations were tested, and, with the exception of *D. Clevelandii,* were found to be reasonably constant for the characters under observation.

In the case of *D. Clevelandii,* the seeds for the parent plants were obtained in the Santa Ana Mountains of western Riverside County from a plant occurring near a small, mixed population of *D. longiflorus, D. Clevelandii,* and their hybrids and derivatives. From the 200 seeds planted, six seedlings appeared and of these only two grew to maturity for use as parent stock. This extremely poor germination and survival might be explained if the

FIG. 26. *Diplacus grandiflorus* × *D. rutilus* F$_1$ No. 107. Grandrutilus Diplacus.

FIG. 27. *Diplacus aridus* × *D. rutilus,* F_1 No. 100. Blanche McInnes Diplacus.

TABLE 3. CROSS-HYBRIDIZATION



seed parents were derived from distantly related entities having relatively weak intercompatibility. Such an hypothesis is supported by the high percentage of sterile pollen produced by the wild seed parent and the two progeny, as well as by the differential survival value of garden-grown seedlings from wild hybrid populations of *D. longiflorus* × *D. Clevelandii*. Under garden conditions those seedlings showing morphological characters of *D. longiflorus* thrived, while those apparently having more genes of *D. Clevelandii* soon died. In the field, very few of the plants in the hybrid population could be identified, upon morphological characters, as *D. Clevelandii*; most of them appeared intermediate or more closely resembled *D. longiflorus*.

The objective of producing more striking garden ornamentals was furthered by crossing the three red-flowered entities, *D. parviflorus, D. puniceus,* and *D. rutilus,* with those of the yellow- and buff-flowered groups which possessed certain characteristics desirable in garden plants. At the present writing, several of these crosses have shown sufficient potentialities as garden subjects to warrant further crossing and selection. Two of these, Grandrutilus Diplacus (*D. grandiflorus* × *D. rutilus*) (fig. 26) and Blanche McInnes Diplacus (*D. aridus* × *D. rutilus*) (fig. 27) have already been described by McMinn (1949). These and other undescribed hybrids are discussed in the section on Garden Culture and Horticultural Possibilities.

One of the primary aims of taxonomic botany is to discover the degree of relationship that exists among the members of a given group of plants. In recent years, artificial hybridization experiments have been recommended and extensively used by Clausen, Keck, and Heisey (1939, 1940), Stebbins (1942, 1950), Grant (1950), Mayr (1942), Epling (1947a, b), Dobzhansky (1941), and many other workers in plant and animal taxonomy as an important technique in revealing these relationships.

In order to ascertain the relationships among the field entities of *Diplacus,* numerous crosses involving eleven of these entities were made (Tables 3 and 4). Some of the F_1 progeny were "selfed", others were backcrossed to one or both parental types, and a few were outcrossed to other parents. For identification purposes, numbers 1 to 99 were given to the parents, 100 to 199 to the F_1 hybrids, 200 to 299 to the F_2 plants, 300 to 399 to backcross progeny, and 400 to 499 to plants resulting from outcrossing.

Explanation of Table 3.

Table 3. Artificial Crosses. Graphic representation of artificial crosses showing parents and F_1 hybrids (the latter indicated by identification number assigned in the culture records.) Numbers adjacent to a given parent indicate that this parent was the female in the cross. For example, in the cross between *D. puniceus* and *D. longiflorus,* the female parent for F_1 progeny nos. 109 and 111 was *D. puniceus* and the male parent was *D. longiflorus.* F_1 progeny nos. 108 and 110 represent hybrids resulting from the reciprocal cross.

TABLE 4. COMPARISON OF TWELVE CHARACTERS IN THE PARENTS AND F_1 HYBRIDS FOR EACH CROSS MADE (The numbers following the parents and the progeny are the identification numbers assigned in the culture records as outlined in the text.)

CROSSES	PEDICEL LENGTH (inches)	CALYX shape surface color	COROLLA color	COROLLA TUBE	COROLLA LOBES	UPPER BRANCHLETS & LOWER LEAF SURFACE	POLLEN FERTILITY (per cent)	SEED GERMINATION	VEGETATIVE VIGOR
aridus 4-4	1/4 ±	flared; glabrous; yellow-green	lemon-yellow	exserted	recurved or rotate	glabrous	95-100; 40-60 in some garden plants	good	vigorous
X									
rutilus 1A-1	1/4 ±	large, swollen; hairy ±; reddish ±	dark velvety red	included	3 lower extend forward	hairy	91-100 (75)	"	"
F_1 100 (fig. 27)	1/4 ±	slightly flared; glabrous ±	tricolored: grayed-red, yellow, cream	exserted ±	rotate to recurved	glabrous to puberulent	95-100 (80)	"	vigorous healthy
aridus 4-2	1/4 ±	flared; glabrous; yellow-green	lemon-yellow	"	recurved or rotate	glabrous	95-100; 40-60 in some garden plants	"	"
X									
parviflorus 1-1	3/8-1	trim; glabrous; tinged red ±	red over yellow	included	extend forward	"	95-100 (60, 77, 85)	"	"
F_1 157, 158								fair	apparently healthy
reciprocals 155, 156								good	vigorous

aridus 4-2 X	1/4 ±	flared; glabrous; yellow-green	lemon-yellow	exserted	recurved or rotate	glabrous	95-100	good	vigorous
puniceus 3-1	1/2-1	trim; glabrous; reddish ±	red over yellow	included	3 lower extend forward	"	90-99	"	"
F_1 102	1/2 ±	trim; glabrous; reddish ±	inter-mediate	exserted ±	rotate to recurved	"	98 ± (90)	"	"
reciprocal 103	1/2 ±	trim; glabrous; reddish ±	inter-mediate	"	"	"	0 - 5 for 18 plants; 2 plants 70	"	"
aurantiacus 7-2 9-2 10-1 X	1/4 - 3/4	trim; glabrous; tinged with red ±	orange	included	3 lower extend forward	" ±	98 ± (73, 85)	"	"
puniceus 3-1	1/2-1	"	red over yellow	"	"	"	90-99	"	"
F_1 148, 149, 162	1/2-1	"	orange with red	"	"	" ±	98 ±	"	"
reciprocal 160								seed good none planted	
calycinus 10-2 10-3 X	1/4 ±	flared; hairy; green	lemon-yellow	exserted ±, rarely included	rotate or 3 lower extend forward	hairy	90-100 (50, pollen giant to small)	good	vigorous
parviflorus 1-1	3/8-1	trim; glabrous; tinged red	red over yellow	included	extend forward	glabrous	95-100 (60, 77, 85)	"	"

TABLE 4. CONTINUED

CROSSES	PEDICEL LENGTH (inches)	CALYX shape surface color	COROLLA color	COROLLA TUBE	COROLLA LOBES	UPPER BRANCHLETS & LOWER LEAF SURFACE	POLLEN FERTILITY (per cent)	SEED GERMINATION	VEGETATIVE VIGOR
F_1 118, 120	1/2-1	trim; glandular-pubescent	mostly intermediate	slightly exserted	3 lower extend forward	glabrous to pubescent ±, glandular	80-86	good	vigorous
		Considerable more variation in all characteristics than in most crosses.							
reciprocals 116, 119, 123	3/8-3/4	slightly flared to trim; glandular-pubescent	more yellow than intermediate	exserted ± to included	3 lower extend forward	glabrous to glandular-pubescent ±	74-90	#123 good	die within 2 years
		Considerable more variation in all characteristics than in most crosses.							
calycinus 10-3 X	1/4 ±	flared; hairy; green	lemon-yellow	exserted ± rarely included	rotate	hairy	90-100 (50, pollen giant to small)	good	vigorous
puniceus 3-1	1/2-1	trim; glabrous; tinged red ±	red over yellow	included	3 lower extend forward	glabrous	90-99	"	"
F_1 122	1/2 - 3/4	trim to slightly flared; hairy ±; glandular	more yellow than intermediate	included to slightly exserted	"	"	82	"	healthy

Clevelandii 2-2 X	1/4 ±	bulbous at base; hairy	deep lemon-yellow	included	extend forward	hairy	33 - 50 garden plant; 60 - 95 field plant, pollen large and small	poor	vigorous
rutilus 1A-1	1/4 ±	large, swollen; hairy; tinged red	deep velvety red	"	3 lower extend forward	"	91-100 (75)	good	"
F_1 147	1/4 ±	swollen; hairy; tinged red ±	burnt-orange to inter-mediate	"	"	" ±	50-65	ca.70%	die within 2 years
Clevelandii 2-2 X	1/4 ±	bulbous at base; hairy	deep lemon-yellow	"	extend forward	hairy	33-50 garden plant; 67-95 field plant	poor	vigorous
grandiflorus 5-14	1/4 - 3/8	trim; glabrous	warm buff	slightly exserted	3 lower extend forward, deeply bifid	glabrous	95-98	good	"
F_1 154	Two capsules developed, but no seed.								
reciprocals 152, 153								good	

TABLE 4. CONTINUED

CROSSES	PEDICEL LENGTH (inches)	CALYX shape surface color	COROLLA color	COROLLA TUBE	COROLLA LOBES	UPPER BRANCHLETS & LOWER LEAF SURFACE	POLLEN FERTILITY (per cent)	SEED GERMINATION	VEGETATIVE VIGOR
fasciculatus 4-6 X	1/4 - 3/8	trim; glabrous; green	warm buff with orange	slightly exserted	3 lower extend forward, deeply bifid	glabrous	90-100	good	vigorous
rutilus 1A-1	1/4 ±	swollen; hairy	dark red	included	3 lower extend forward, not deeply bifid	hairy	91-100	"	"
F_1 151	1/4 ±	large, swollen; slightly hairy	red-copper	"	bifid, with secondary lobe	glabrous to slightly hairy		excellent	"
grandiflorus 5-16 X australis 11-6	1/4 - 3/8	trim; glabrous; green	warm buff	slightly exserted	deeply bifid	glabrous	95-99	"	"
	1/4 - 3/8	trim; glabrous; tinged red	buff to orange-yellow	included	not bifid	"	98-100 (53, 57, 70-92)	"	"
F_1 145	1/4 - 3/8	trim; glabrous; green	intermediate = light apricot	included to slightly exserted	"	"		good	"

grandiflorus 5-4 X Clevelandii 2-2	Characters as previously given.							good poor	vigorous frail to vigorous
F_1 130	3 poor capsules with undeveloped seed								
grandiflorus 1-1 X	1/4 - 3/8	trim; glabrous; green	warm buff	slightly exserted	bifid	glabrous	95-99	good	vigorous
parviflorus 1-1	3/8 - 1	trim; glabrous; tinged red	red over yellow	included	not bifid	"	95-100 (60, 77, 85)	"	"
F_1 114	1/4 - 1/2	trim; glabrous; tinged red	intermediate, yellow-red	included to slightly exserted	not bifid or intermediate	"	30 ±, pollen scarce, giant to small	"	"
reciprocal 115	1/4 - 3/4	trim; glabrous; tinged red	more red-yellow	"	"	"	50	excellent	"
grandiflorus 1-1 X	1/4 - 3/8	trim; glabrous; green	warm buff	slightly exserted	bifid	"	95-100	"	"
puniceus 3-1	1/2 - 1	trim; glabrous; tinged red	red over yellow	included	not bifid	"	90-99	"	"

TABLE 4. CONTINUED

CROSSES	PEDICEL LENGTH (inches)	CALYX shape surface color	COROLLA color	COROLLA TUBE	COROLLA LOBES	UPPER BRANCHLETS & LOWER LEAF SURFACE	POLLEN FERTILITY (per cent)	SEED GERMINATION	VEGETATIVE VIGOR
F_1 113	1/4 - 1/2	trim; glabrous; tinged red ±	intermediate on red side	included to slightly exserted	not bifid	glabrous	50 ±	excellent	vigorous
reciprocal 112	1/4 3/4	"	intermediate	"	"	"	0 - 2; another without pollen	"	"
grandiflorus 1-1 X rutilus 1A-1	1/4 - 3/8	trim; glabrous; green	warm buff	slightly exserted	bifid	"	95-100	good	"
	1/4 ±	swollen, large; hairy	dark red	included	not bifid	hairy	91-100 (75)	"	"
F_1 107 (fig. 26)	1/4	swollen, large; glabrous ± to glandular-hairy	intermediate	included, or few exserted ±	bifid ± or not	nearly glabrous	81-95	"	"
reciprocals 104, 106, 125-1	1/4	swollen, large; glabrous to glandular-hairy	"	"	"	"	"	"	"

grandiflorus X rutilus 1A-1 = F_1 142 5-12	Same as above.							good	vigorous
grandiflorus X rutilus 1A-1 = F_1 143 5-13	Same as above.							"	"
grandiflorus X rutilus 1A-1 = F_1 128 5-14	Same as above. 128-2,-4 fls. nearly pink							"	"
longiflorus 3-1 X	1/4 ±	large, swollen; hairy	yellow	included	3 lower extend forward	hairy	98 ±	"	"
parviflorus 1-1	3/8 - 1	trim; glabrous; tinged red	red over yellow	"	extend forward	glabrous	95-100 (60, 77, 85)	"	"
F_1 126	1/4 - 1/2	trim; glabrous; tinged red ±	inter-mediate	"	3 lower extend forward	"	53 ±	fair	"
reciprocal 124	1/4 - 1/2	trim; glabrous; tinged red	on yellow side to orange-red	"	"	glabrous ±	28 ±	"	"
longiflorus 7-4 X	1/4 ±	large, swollen; hairy; green	orange	"	"	hairy	98 ±	good	"
puniceus 3-1	1/2 - 1	trim; glabrous; tinged red	red over yellow	"	"	glabrous	90-99	"	"

TABLE 4. CONTINUED

CROSSES	PEDICEL LENGTH (inches)	CALYX shape surface color	COROLLA color	COROLLA TUBE	COROLLA LOBES	UPPER BRANCHLETS & LOWER LEAF SURFACE	POLLEN FERTILITY (per cent)	SEED GERMINATION	VEGETATIVE VIGOR
F_1 108	1/2 ±	trim; glabrous ±; tinged red	intermediate orange-red	included	3 lower extend forward	nearly glabrous	92	good	vigorous
reciprocal 109	1/4 ± to 3/4 -	trim; glabrous; tinged red	"	"	"	"	91	"	"
longiflorus 3-3 X puniceus 3-1	1/4 ±	large swollen; hairy; green	yellow-orange	"	"	hairy	98 ±	"	"
	1/2 - 1	trim; glabrous; tinged red	red over yellow	"	"	glabrous	90-99	"	"
F_1 110	1/4 ± to 3/4	trim; glabrous ±; tinged red	intermediate	"	"	nearly glabrous	95	"	"
reciprocal 111	1/4 ± to 1	trim; glabrous; tinged red	"	"	"	"	67-90	excellent	"
rutilus 1A-1 X fasciculatus 4-12 F_1 159	See cross fasciculatus 4-6 X rutilus 1A-1 for characteristics. Excellent seed germination; plants healthy and vigorous.								
Clevelandii 2 x longiflorus 3, Clevelandii 2 x parviflorus 1, Clevelandii x puniceus: no seed.									

Ten of the eleven field entities used as parents, *D. aridus, aurantiacus, australis, calycinus, fasciculatus, grandiflorus, longiflorus, parviflorus, puniceus,* and *rutilus,* proved to be quite self-compatible and produced abundant and viable seed with their own pollen. The eleventh, *D. Clevelandii,* set very few fertile seeds when "selfed" or crossed with other entities. It also produced very few mature capsules when left for open pollination.

Viability of pollen grains in populations of ten of the parent plants was tested for three consecutive years and was found to be from 95 to 100 per cent viable, in most cases. The pollen of *D. Clevelandii,* however, was only 33 to 50 per cent viable for the two garden plants and 60 to 95 per cent viable for the wild parent plant. Lessened viability of pollen in garden-growth plants was also noted in *D. aridus, D. calycinus,* and *D. parviflorus.*

Methods of Hybridization. Because of their size and the ease of determining maturity of the anthers and stigmas, crossing the flowers in *Diplacus* is a relatively simple operation. At the tip of the style is the flattened stigma, its two glandular-pubescent stigmatic surfaces remaining closely appressed against one another until maturity, when through the elongation of the style they have reached a position slightly above the longer pair of stamens. These stigmatic lobes then open and remain so for two or three days unless irritated by pollen or foreign substances. The anthers ripen at about the same time as the stigma, or, at most, only a day or so later than the spreading of the stigmatic lobes. Because of the position of the stigmatic lobes, self-pollination would hardly be expected unless brought about by the numerous bees, beetles, flies, and other insects, and even humming birds which visit the flowers.

Pollination was accomplished by applying pollen to the stigmatic surfaces with forceps or by touching them with the ripe anthers from the desired male plant. The stamens of the pollinated flowers were then removed and a wax paper bag was placed over the flowers to prevent insect pollination. Stigmas which were receptive to the pollen remaind closed; otherwise they re-opened and could be re-pollinated.

The F_1 Hybrids. All crosses undertaken, except some involving *D. Clevelandii,* were successful (see tables 3 and 4). The pollen of the F_1 hybrids and of the reciprocals was for the most part as viable as that of their parents. The exceptions were: F_1 hybrid *D. grandiflorus* × *D. parviflorus* (No. 114), which had scant pollen only about 30 per cent viable, some of these grains being of exceptionally large size; the reciprocal *D. parviflorus* × *D. grandiflorus* (No. 115), which had pollen about 50 per cent viable; F_1 hybrid *D. grandiflorus* × *D. puniceus* (No. 113), which had about 50 per cent viable pollen; the reciprocal *D. puniceus* × *D. grandiflorus* (No. 112), which had practically no viable pollen, one flower having no pollen in any of its four anthers; F_1 hybrid *D.*

longiflorus × *D. parviflorus* (No. 126), which had about 53 per cent viable pollen; the reciprocal *D. parviflorus* × *D. longiflorus* (No. 124), which had about 28 per cent viable pollen; and the reciprocal *D. puniceus* × *D. aridus* (No. 103), which had 0 to 5 per cent fertile pollen for 18 plants and about 70 per cent fertile pollen for two plants. The cross *D. aridus* × *D. puniceus* (No. 102) had 90 to 98 per cent fertile pollen.

It is worthy of note that in the two crosses *D. aridus* × *D. puniceus* and *D. puniceus* × *D. grandiflorus,* the pollen fertility was greatly reduced for its reciprocals. Reciprocal differences in sterility of hybrid pollen have been reported also by Grant (1950) for *Gilia,* by Skalinska (1928) for *Aquilegia,* and by Lehmann (1931) and Michaelis (1933) for *Epilobium.*

In those crosses involving *D. Clevelandii,* it was found that *D. Clevelandii* was not receptive to pollen of *D. grandiflorus, D. longiflorus, D. parviflorus,* and *D. puniceus,* but was receptive to pollen of *D. rutilus.* Pollen of *D. Clevelandii* on *D. grandiflorus* (No. 5-14) was effective and many viable seeds were formed, but the same pollen on *D. grandiflorus* (No. 5-4) was ineffective. The pollen of the garden plant of *D. Clevelandii* was only 33 to 50 per cent viable, but this should not necessarily account for the difference of pollen receptivity by the two different parents of the same lot of *D. grandiflorus.* Further crossings should be carried on before speculations and conclusions are made.

Seed germination of the F_1 hybrids was in most cases equal to that of the parents, and the mature hybrid plants were healthy and vigorous. Observations on intercompatibility, pollen fertility, seed germination, and vigor of hybrid plants all indicate that the entities concerned are very closely related. (See section on Biological Relationships and Evolution.)

Inheritance of Characters. Although a study of the hereditary behavior of characters was not one of the primary aims of the investigations, a few pertinent observations will nevertheless be given. The pedicel-length in *D. parviflorus* and *D. puniceus* typically varies from ½ to 1 inch long, in *D. aurantiacus* it varies from ¼ to ¾ inch long, and in all other entities its length is about ¼ inch. In crosses involving entities with the long and the short pedicel, the long pedicel appeared dominant. The three entities with red flowers, *D. parviflorus, D. puniceus,* and *D. rutilus,* when crossed with entities of yellow- or buff-colored flowers, produced intermediate flower color in all cases. In subsequent hybrids, many hues of various intensities appeared, thus suggesting that flower color was the result of multiple factors rather than of a single dominant one. The corolla-tube of *D. aridus* is extended beyond the calyx, and in *D. calycinus* it is also more or less exserted. When these were crossed with entities in which the corolla-tube is included, the results were such that the character of the exserted tube appeared to be dominant in F_1 hybrids. The

TABLE 5. COMPARISON OF FIVE CHARACTERS OF D. LONGIFLORUS AND D. PARVIFLORUS AND THEIR F_1 HYBRIDS (AVERAGE FOR 100 FLOWERS).

PLANT	PEDICEL LENGTH	FLOWER LENGTH	FLOWER WIDTH	FLOWER COLOR	CALYX SURFACE
D. longiflorus 3-1	5.8 mm	34 mm	33 mm	yellow	pubescent to hairy
D. parviflorus 1-1	11 mm	30 mm	16 mm	orange-red	glabrous
F_1 = 126	10 mm	35 mm	21.8 mm	blend	glabrous
Reciprocal = 124	9.8 mm	35 mm	23 mm	blend	glabrous

upper branchlets and lower leaf-surfaces are noticeably pubescent to hairy in *D. longiflorus, D. calycinus,* and *D. rutilus.* Whenever these entities were crossed with glabrous or nearly glabrous forms, the F_1 hybrids were glabrous to only slightly pubescent, thus indicating that the factor for glabrousness is dominant over that producing the pubescent condition. Various degrees of pubescence were observed in F_2 and other hybrids. *Diplacus aridus* has recurved or rotate corolla-lobes, and when crossed with *D. rutilus, D. parviflorus,* and *D. puniceus,* which have the three lower lobes extended forward, the rotate or recurved condition was dominant in the F_1 hybrids. The behavior of a few other characters is recorded in tables 4 and 5 and in the summaries of the F_2 and other hybrids.

F_2 Hybrids. F_2 seeds and seedlings were observed from 36 crosses which involved the "selfing" of 17 F_1 hybrids. From observations on the first germination trials, it appeared that a lessened viability of seed had occurred, but there was considerable delayed germination and this when combined with the germination that occurred in later tests totaled about the same as for the parent and F_1 hybrid seeds. Owing to insufficient numbers of F_2 hybrid plants and to the amount of labor and time involved, the behavior of factors for characters observed in the F_2 generation was not analyzed. From the seventeen cases which were observed and recorded, it would appear that an indefinite number of recombinations had taken place.

Backcrosses and Outcrosses. Eight backcrosses, three reciprocal backcrosses and twelve outcrosses were made. Results of these crosses were recorded and are available for reference at Mills College.

Before concluding the section on Artificial Hybrids in *Diplacus,* I shall give a brief account of the known hybridization work of others.

Lemaire (1863) reported crosses between *D. aurantiacus* (yellow-flowered) and *D. puniceus* (red-flowered) with *D. glutinosus* (yellow-flowered) under the names *D. glutinosus* var. *Godroni, D. glutinosus* var. *splendidus,* and *D. glutinosus* var. *Verschaffeltii.* Vershaffelt later (1863) raised Lemaire's varieties to specific rank. The sources of the material are not indicated and the actual field entities involved are unknown. The two taxa, *D. glutinosus* and *D. aurantiacus,* mentioned in the crosses, are now considered synonymous. Whatever may have been the parentage of these hybrids, they apparently crossed freely and gave variable offspring. The author reports all three hybrids as having deep red corollas. In my experience, whenever a red-flowered parent is crossed with a yellow-flowered one, intermediate flower color results. In order to obtain red-flowering plants from such crosses, I have found it necessary to backcross with the red parent or to "self" the F_1 generation.

Dr. Adele Grant (1924) reports upon some unpublished work done by Dr. Love Miller while the latter was a graduate student at the University of California at Berkeley. She states that, "Dr. Miller crossed a plant of *M. longiflorus* from near Los Angeles with a plant of *M. puniceus* from near San Diego. With *M. puniceus* as the female parent, the cross was successful; the reciprocal cross, however, gave no results. In plants of the first generation were combined characters of both parents, as would be expected. . . . The plants produced little pollen so that it was difficult to get seed from self-pollinated flowers. Nevertheless, some were obtained and plants of the F_2 generation showed red, yellow, and salmon flowers, the salmon ones being the most abundant."

The results of my hybridization of these two parents are in general agreement with those of Dr. Miller. A few characters, however, such as length of pedicel and shape of calyx, instead of being intermediate in F_1 were like the *D. puniceus* parent. I also found that the reciprocal cross was successful, and that both crosses produced much good pollen. There is a possibility that the climatic conditions in East Oakland may be better than in Berkeley for such experiments.

Dr. Grant (1924) also pointed out that natural hybrids apparently occur in this group of plants, citing collections of P. A. Munz, Ivan Johnston, Robert Harwood, H. M. Hall, L. R. Abrams, W. L. Jepson, D. Cleveland, A. L. Grant, and others to support this view.

Mr. Victor Reiter, Jr., of San Francisco made a few crosses

in 1935, but the sources of the parents could not be determined and no published records were made.

Mr. F. F. Gander of Lakeside, San Diego County, made a cross between a plant transplanted from Montezuma Valley between Warner's Stage Station and the Borego region, San Diego County, and *D. australis,* a transplanted plant from near Julian, San Diego County. The Montezuma Valley plant was thought to have been *D. aridus,* but examination of the plants in Mr. Gander's garden leads me to believe the parent (*H. E. McMinn & M. Van Rensselaer, 1901*) may have been a hybrid between *D. aridus* and *D. calycinus,* or even probably a form of the southern *D. calycinus.* The calyces were flared like those of *D. aridus,* but hairy as in *D. calycinus.* The lemon-yellow corollas with exserted tubes and rotate to recurved limbs are characters shared by both of these entities. The plant from Spencer Valley (*H. E. McMinn & M. Van Rensselaer, 1902*), had glabrous, trim calyces and orange-lemon corollas, the tubes of which were included and with the limb not rotate or recurved. In general appearance the F_1 plant, No. 1903, resembled the parent plant from Montezuma Valley, but the flowers were larger, the corolla-lobes were not recurved, the corolla-tube was not exserted, and the calyces were less hairy. F_1 plant, No. 1904, resembled the parent from Spencer Valley, but had some pubescence on the calyces and on the lower surfaces of upper leaves. Since the two F_1 hybrid plants were so different from each other, it would appear that one of the parents must have been a hybrid.

Garden Hybrids. Wherever two or more natural entities have been grown in gardens which have not been too carefully cultivated, spontaneous hybrids usually occur. Such hybrids have been observed in the Santa Barbara Botanic Garden, at the Rancho Santa Ana Botanic Garden, Tilden Regional Park, in the Mills College native plant collection, and in smaller privately owned gardens. By careful study of these hybrids, it is usually possible to work out the probable natural entities involved, even though these entities may not at the time be growing in the gardens.

In the Santa Barbara Botanic Garden, an exceptionally fine group of hybrids, involving the field entities *D. aurantiacus, D. longiflorus, D. australis, D. puniceus,* and *D. rutilus,* has been grown for several years. They display an extraordinary range of color in which forty-two hues have been determined by the Art Department of the University of California, Santa Barbara College. The results of their determination were later published by Mr. M. Van Rensselaer (1944).

Probable Biological Relationships and Evolution

Rarely, if ever, is one able to bring together sufficient evidence to present the true evolution of any group of biological forms, and

the genus *Diplacus* is no exception. However, from the studies of field and artificial hybrids, cytology, comparative morphology, and geographical distribution, certain observations have been made which seem to indicate definite relationships and trends of evolution among the existing entities. It appears that hybridization of the introgressive type has played a prominent role in the evolution of this group. Important as this may have been in the evolution of the numerous field forms, there is no definite evidence that the four entities placed at the bottom of the phylogenetic chart (table 6) have arisen by this method.

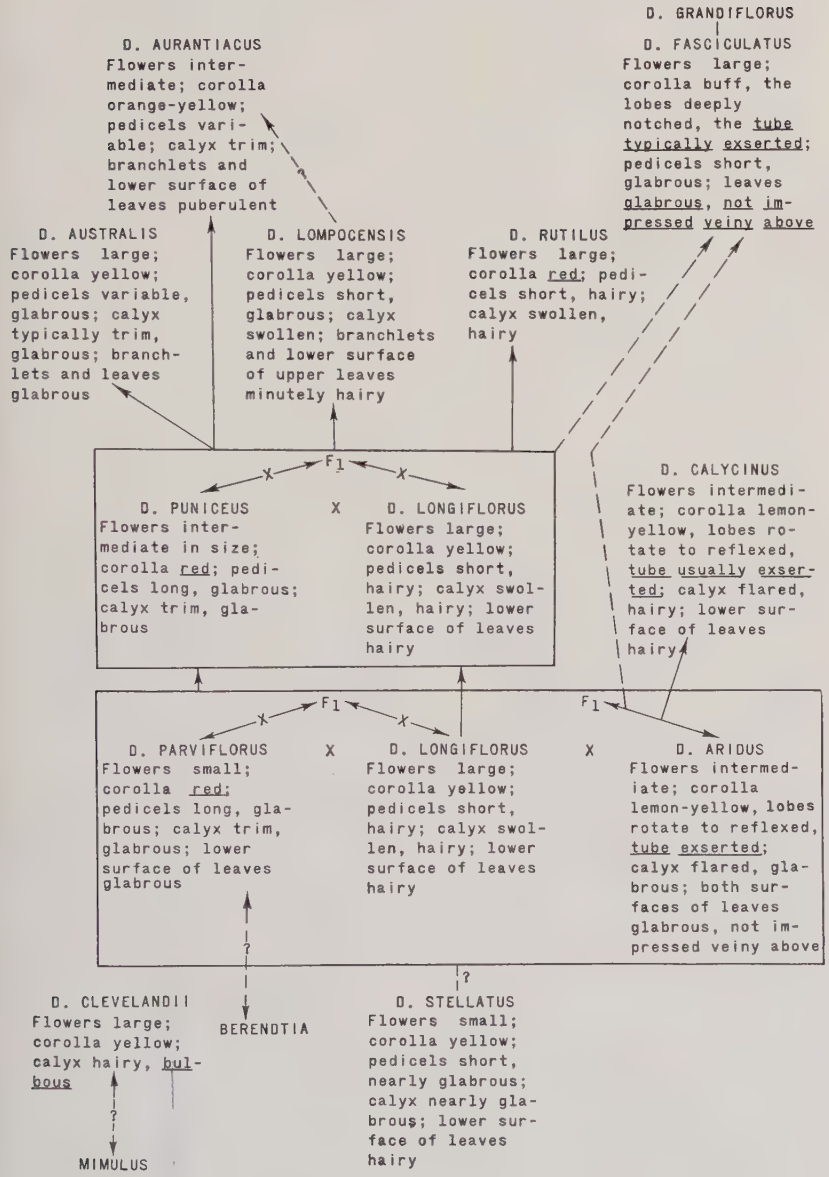
A study of the phylogenetic chart reveals that *D. Clevelandii* stands apart from the other entities. The nearly herbaceous nature of the plant, the dehiscence of the capsule along four lines instead of one or two, the bulbous calyces, and the type of exudation are characters not found in other field entities in the genus *Diplacus*. When we consider the difficulty of producing artificial hybrids with *D. Clevelandii* as one of the parents, these characters are sufficient reasons for setting this entity apart as a distinct taxonomic "species." Only in the case of the few natural hybrids formed between *D. Clevelandii* and *D. longiflorus* is there any evidence that genes of *D. Clevelandii* have entered into the evolution of the remainder of the group.

Diplacus parviflorus is probably one of the most ancient of the existing entities. In the configuration of the leaves and flowers this entity has much in common with *Berendtia laevigata,* a species native to Mexico. The possibility that the genus *Berendtia* or some common ancestor may be ancestral to the genus *Diplacus* cannot be ruled out entirely.

The long glabrous pedicel, the slim glabrous calyx, the red-over-yellow corolla, and the glabrous herbage of *D. parviflorus* are characters which appear in *D. puniceus,* an entity which probably segregated out of a population in which *D. parviflorus* was involved. The more erect habit, larger flowers, and configuration of the leaves of *D. puniceus* are characters for which the source of genes is probably some extinct ancestral form which entered into a population with *D. parviflorus.*

The characters of the short pedicel, various hues of yellow flowers, pubescence of upper stems, branches, pedicels, and calyces, and larger flowers which appear in several field entities may be accounted for by genes from *D. longiflorus,* an entity which may be considered primitive. Whatever may have been the origin of *D. puniceus* and *D. longiflorus,* we have in these two entities genes which have entered and are continuing to enter into natural hybrids in southern California wherever the two parents grow together. I can conceive of past hybridization having taken place somewhere in what is now southern California at a time when the coastal islands were a part of the mainland. As the progeny of these crosses multiplied and backcrossed

TABLE 6. PROBABLE RELATIONSHIPS AND EVOLUTION IN DIPLACUS



with the parents, many new combinations of genes occurred. The plants containing these genes migrated from their centers of origin and inhabited new areas, there to segregate into new entities which possessed the best combination of genes suited for the different new habitats. At that time, new populations were separating from the polymorphic parental population. That some of this type of segregation is still going on cannot be denied. From these older populations, such present-day entities as *D. australis, D. aurantiacus, D. lompocensis,* and *D. rutilus* may have been derived.

Since many of the characters of these field entities are probably each due to several factors operating simultaneously which are, therefore, quantitative factors, it is not possible to point out more than their closest probable relatives. *Diplacus australis* of southern California, *D. lompocensis* of Santa Barbara County, and *D. aurantiacus* of northern California, although closely resembling each other, can be distinguished by a few characters which seem to breed true when any one of the three entities is "selfed." The various intensities and values of yellow hues of the flowers relate the three entities to *D. longiflorus,* while the glabrous or subglabrous nature of calyces and pedicels relates them more closely to *D. puniceus. Diplacus lompocensis* has so many characters in common with *D. longiflorus* that it might be considered a nearly glabrous form of that entity occupying a distinct geographical area. Since this geographical area is one which occurs between the southern distribution of *D. aurantiacus* and *D. fasciculatus* × *D. aurantiacus* and the northern distribution of *D. longiflorus* in Santa Barbara County, it might be better to consider *D. lompocencis* a rather recent "subspecies" which has segregated out of a population in which these three entities have been involved. The typically slender calyces of *D. aurantiacus* and *D. australis* relate these two more closely to each other and to *D. puniceus* than to *D. longiflorus* or *D. lompocensis,* which have broader, somewhat swollen calyces. The width of the corolla-spread of *D. aurantiacus* relates it to *D. puniceus,* while the spread of the corollas of *D. australis* and *D. lompocensis* more closely approximates that of *D. longiflorus.*

Diplacus rutilus, except for the deep velvety-red color of its corollas, possesses most of the characteristics found in *D. longiflorus.* The red pigment may be due to a factor or factors from *D. puniceus* or its red-flowered ancestors, and from breeding experiments it appears to be homozygous for color. Since *D. rutilus* is easily distinguished from *D. longiflorus* by this pigment, and since it is interfertile with that entity and is always found in association with *D. longiflorus* or its hybrids and not in a separate geographical area, it may be considered an incipient "subspecies."

Diplacus aridus occurs in southeastern San Diego County. The probable origin of this entity is not clear. Its characters of

flared calyces, light lemon-yellow flowers, exserted corolla-tubes, and rotate to recurved corolla-lobes are not found in any of the other entities thus far mentioned. However, this combination of characters does occur in *D. calycinus,* an entity which probably resulted from crosses involving *D. aridus* and *D. longiflorus.* The character of hairy upper branchlets, pedicels, and calyces, found in *D. calycinus,* is probably due to genes from *D. longiflorus.* The geographical distribution of these entities does not preclude such an origin for *D. calycinus.*

The two natural entities *D. fasciculatus* and *D. grandiflorus* appear to be the last ones evolved. I have not been able to account for their probable origin by hybridization alone. Both have large corollas with the lobes deeply notched, a character not found in any of the other forms. The corolla-tube is usually somewhat exserted, a condition found in *D. aridus* and *D. calycinus.* The warm buff-colored flowers, although larger, resemble somewhat those of *D. lompocensis.* The upper surfaces of the leaves are not at all impressed-veiny, a condition found also in *D. aridus* and *D. parviflorus.*

Diplacus stellatus has been collected only from Cedros Island and is not sufficiently well known to place it in its proper position in an evolutionary sequence. It has certain characters such as size of flower, leaf-shape, and curve in the corolla-tube which relate it to *D. parviflorus,* but the characters of yellow flowers and the pubescence of the upper branchlets, pedicels, and under surfaces of the leaves relate it to *D. longiflorus.* It may be a relic of an early segregation from forms ancestral to both of these related entities.

Results obtained from studies in geographical distribution and the application of the sterility test, recommended by Clausen, Keck, and Hiesey (1939) and others for designating specific rank to the field entities, indicate that there may be only two distinct species (ecospecies) in the genus *Diplacus,* namely *D. Clevelandii* and *D. aurantiacus.* All the other entities given binomial rank, except *D. stellatus* which was not available for testing and × *D. linearis,* would then be classified as subspecies. With the exception of *D. rutilus,* which may be considered an incipient subspecies, all the fertile interbreeding entities occupy different geographical areas and therefore fulfill one of the major requirements for a subspecies.

Attempted crosses involving *D. Clevelandii* were only partially successful, and the progeny from these produced much sterile pollen, their seeds germinated poorly, and the few plants actually produced soon died. The numerous crosses made involving the other entities were nearly one hundred per cent successful. The pollen of the F_1, F_2, and backcross progeny was as fertile in most cases as that of the parents. Seed germination was good and the progeny were as healthy as the parents. (See section on Hybrids.)

Chronological History of the Genus

Since the description of the first entity in 1796, the fourteen entities included in this paper have appeared in publications under at least fifty-eight different binomials or trinomials, either in the genus *Diplacus* or in the genus *Mimulus*. The synonymy for each entity is given in the section on Taxonomic Treatment.

The first known description of any entity in *Diplacus* was published with a colored plate by Wm. Curtis in 1796 under the name *Mimulus aurantiacus*. It was based upon plants grown in England from seeds undoubtedly collected by Menzies in northern California during his visits there in 1792, 1793, and 1794, though the author did not know with certainty the source of the seed from which the plants were grown. The colored plate and description are quite satisfactory for the plants now growing naturally in northern California. These plants are retained in the genus *Mimulus* by some botanists, but others place them in the genus *Diplacus*. In 1798 Johann Christoph Wendland described *Mimulus glutinosus* from a plant also grown in England, but he likewise stated that the source of the seed was not known. Undoubtedly this seed, too, must have come from Menzies' collection or from plants grown from his material, as only Haenke had collected along the California coast up to that time. Conradi Moench in 1802 described *Mimulus viscosus*. These three entities are considered to be the same, and are here included under *Diplacus aurantiacus* (Curt.) Jepson.

George Bentham was the next botanist to recognize a new entity in this group. In his studies of the Scrophulariaceae in 1835, he included two woody Mimuli, *M. linearis* (sp. nov.) and *M. glutinosus* Wendl. (*M. aurantiacus* Curt.). His *M. linearis* was based upon a specimen collected by David Douglas in California. The Douglas specimen appears to the writer to be one of several hybirds between *D. aurantiacus* and *D. fasciculatus* which occur in various localities in Monterey, San Benito, and San Luis Obispo counties. It is known that Douglas collected in coastal central California from Sonoma to Santa Barbara counties.

Thomas Nuttall, the first botanist to study plants of this group in the field, proposed the genus *Diplacus* in 1837 and published it in 1838. In establishing the genus, Nuttall emphasized the woody nature of the plants and the characters of the fruit. He states that, "The generic name alludes to the splitting of the capsule, attached to each valve of which is seen a large placenta, and under its edges are found slender subulate seeds." He transferred *Mimulus glutinosus* Wendl. to the new genus and described four new entities, *D. puniceus, D. latifolius, D. longiflorus,* and *D. leptanthus,* the first three based upon material which he collected in California, the fourth based upon material collected by Menzies in California. *Diplacus latifolius, D. leptanthus,* and *M. glutinosus* have since been reduced to synonymy. *Diplacus puniceus* and *D. longiflorus* are considered here as distinct entities.

In 1846, eight years after the publication of the genus *Diplacus,* George Bentham transferred his *M. linearis* to *Diplacus,* and also included three other entities, *D. rugosus* (sp. nov.), *D. glutinosus* Nutt., and *D. longiflorus* Nutt. He considered his *M. linearis* to be the same as Nuttall's *D. leptanthus* and dropped his prior species name in favor of *leptanthus,* a policy not permitted by the present rules of nomenclature. Examination of the type specimens for these two names and knowledge of the plants gained from field work leads the writer to consider the two as distinct. Nuttall's *D. leptanthus* is the same as *D. aurantiacus* (Curt.) Jepson, and Bentham's misinterpretation of *D. leptanthus* is × *D. linearis* (Benth.) McMinn, a hybrid produced by the interbreeding of *D. aurantiacus* and *D. fasciculatus. Diplacus rugosus* of Mexico has since been correctly removed from *Diplacus,* having been transferred to the genus *Berendtia.*

Professor John Lindley in 1852–53 described the variety *grandiflorus* of *D. glutinosus,* which he based upon a greenhouse shrub grown from seed collected in California, most likely by Hartweg. The colored plate which accompanies the description is easily recognized as the plant of the northern Sierra Nevada. J. E. Planchon in 1853–54 published, under the name of *D. glutinosus grandiflorus,* a colored plate and a brief description of another English-grown plant which appears definitely to represent these northern Sierra Nevada plants. Still another description with a drawing which matches both these previous ones was published independently by J. Grönland in 1857 under the name *D. grandiflorus.* It also was based upon a cultivated plant grown in England. Although the three descriptions, plates, and drawing were made from different English-grown plants, there is no doubt that these plants were grown from seed of the Sierra Nevada plants which I here treat as *D. grandiflorus.*

The next entity to be published was *D. stellatus,* described by Albert Kellogg in 1863 from material collected by J. A. Veatch on Cedros Island. It is a little known and rarely collected entity of uncertain status. In the same year, Ambroise Verschaffelt described three garden hybrids (apparently between *D. aurantiacus* and *D. puniceus* with *D. glutinosus*). Later in the year Charles Antoine Lemaire included these as varieties of *D. glutinosus.*

In 1876, Asa Gray, in his systematic treatment of the genus *Mimulus,* in two different publications within the same year, reduced Nuttall's genus *Diplacus* to a section of *Mimulus* in which he included *M. glutinosus* Wendl. with the vars. *puniceus* (Nutt.), *linearis* (probably some hybrid of *D. longiflorus* with *D. puniceus*) not Benth., and *brachypus,* a new name for *D. longiflorus* Nutt. In the same year, George Bentham and Wm. Hooker included *Diplacus* as a section of *Mimulus.* In Gray's further studies in *Mimulus,* published in 1878, he retained the same treatment for the section *Diplacus* as that in his two 1876 publications.

E. L. Greene restored *Diplacus* to generic rank in 1885. He included one new entity, *D. arachnoideus,* based upon material which he had collected at All Saints Bay, Lower California, April 16, 1885, and six previously described ones, *D. stellatus* Kell., *D. glutinosus* (Wendl.) Nutt., *D. latifolius* Nutt., *D. puniceus* Nutt., *D. leptanthus* Nutt., and *D. longiflorus* Nutt. In the following year, 1886, Gray in another revision of the genus *Mimulus* included *Diplacus* as a section in which he raised *M. puniceus* (Nutt.) Steud. to species rank but still retained the varieties *linearis* and *brachypus* under *M. glutinosus* Wendl.

Diplacus parviflorus was described by E. L. Greene in 1887. It was based upon material which he had collected on Santa Cruz Island. Three years later, 1890, Greene prepared a revision of the genus *Diplacus* in which he gave ample reasons for maintaining it as a valid genus rather than as a section of *Mimulus.* In the revision, he maintained *D. glutinosus* (Wendl.) Nutt., under which he placed *D. stellatus* Kell. and *D. latifolius* Nutt. as varieties, *D. longiflorus* Nutt., under which he included his *D. arachnoideus* as a synonym, *D. linearis,* a new combination for *M. linearis* Benth., *D. grandiflorus,* a new name for the northern California plants Greene had confounded with Nuttall's *D. longiflorus, D. puniceus* Nutt., and *D. parviflorus* Greene.

R. v. Wettstein in Engler and Prantl's Die Natürlichen Pflanzenfamilien, 1891, treated *Diplacus* as a section of *Mimulus* in which he included *M. glutinosus* (Nutt.) Wendl., *M. puniceus* (Nutt.) Steud., and *M. rugosus* Benth., the latter an entity now known to be *Berendtia rugosa* (Benth.) Gray. In 1894, J. B. Davy described *D. speciosus* from a plant grown in the botanical gardens at the University of California, Berkeley, but this has been reduced to synonymy under *D. longiflorus* Nutt. In 1895, T. S. Brandegee described a new *Mimulus* from Cuyamaca Peak, San Diego County, as *M. Clevelandii,* which E. L. Greene the following year transferred to *Diplacus.* It is here included as a valid entity, *D. Clevelandii* (T. S. Brandg.) Greene.

Soon after the turn of the century, two new entities were added to *Diplacus.* L. R. Abrams described *D. aridus* in 1905 from plants which he had collected in 1903 in southeastern San Diego County. The following year, Alice Eastwood described *D. calycinus* from material collected by Culbertson in the southern Sierra Nevada. Both of these entities are included here as distinct.

Still another treatment reducing *Diplacus* to a section of *Mimulus* was made by Adele L. Grant in 1924 in her monograph of *Mimulus.* Based upon material which she had collected in Ventura County, she proposed the entity *rutilus* as a new variety of *M. longiflorus.* She also listed a number of natural hybrids under the combination of *M. longiflorus* × *M. puniceus.* In 1925, W. L. Jepson treated *Diplacus* as a valid genus in his Manual of the Flowering Plants of California. He treated Greene's *D. grandiflorus* and

Eastwood's *D. calycinus* as varieties of *D. longiflorus* Nutt., and was the first botanist to give *Mimulus aurantiacus* Curt. its proper recognition under the genus *Diplacus*.

After the publication of the monograph of *Mimulus* by Grant, writers on the western American flora were about equally divided in their acceptance of *Diplacus* as a section of *Mimulus* or as a valid genus. P. A. Munz in 1935, following Grant's usage, proposed the name *M. Flemingii* for *M. parviflorus* (Greene) Grant (1923) since the name *parviflorus* was not tenable under *Mimulus* because of the earlier *Mimulus parviflorus* of Lindley (1825). In an Illustrated Manual of California Shrubs (1939), the present writer, although he did not describe any new entities, made three new combinations in *Diplacus*. F. W. Pennell in 1947 cast his lot with the "section group" by proposing, under *Mimulus*, the name *M. bifidus* for the northern Sierra Nevada plants known as *D. grandiflorus* (Lindl.) Grönl., and the name *M. bifidus* subsp. *fasciculatus* for some little understood Monterey County plants which have been variously treated by previous authors under different species or varieties, but which are herein treated as *D. fasciculatus*.

In this paper the author maintains *Diplacus* as a valid genus, consisting of fourteen named taxa of binomial rank. Nine of them have been previously described under the accepted names *D. aridus, D. aurantiacus, D. calycinus, D. Clevelandii, D. grandiflorus, D. longiflorus, D. parviflorus, D. puniceus,* and *D. stellatus;* three, *Mimulus bifidus* subsp. *fasciculatus* Pennell, *M. longiflorus* var. *rutilus* Grant, and *M. linearis* Benth., are here treated as the binomials *Diplacus fasciculatus, D. rutilus,* and × *D. linearis* respectively; one, *D. lompocensis,* is described as new; and one, *D. linearis* Greene, not Bentham, is newly named *D. australis*.

A summary of the chronological history of the genus follows:

1796 Curtis, Wm. Bot. Mag. I. 10: pl. 354.
1798 Wendland, Johann Christoph. Bot. Beobacht. 51.
1802 Moench, Conradi. Meth. Pl. Hort. Marburg., Suppl. 168.
1835 Bentham, George. Scroph. Ind. 27.
1838 Nuttall, Thomas. Ann. Nat. Hist. I: 137.
1846 Benthan, George. DC. Prodr. 10: 368.
1852–53 Lindley, John. Paxt. Fl. Gard. 3: pl. 92, opp. p. 95.
1853–54 Planchon, J. E. Fl. Des. Ser. et des Jardins 9: pl. 883 (colored), facing p. 71.
1857 Grönland, J. Paris Rev. Hort. IV. 6: 402–404, fig. 136, p. 403.
1863 Kellogg, Albert. Proc. Calif. Acad. ser. I, 2: 18.
1863 Vershaffelt, Ambroise. Belg. Hort. 13: 4.
1863 Lemaire, Charles Antoine. L'Illust. Hort. 10: pl. 359, figs. 1, 2, 3.
1876 Gray, Asa. Proc. Am. Acad. 11: 97.
1876 Gray, Asa. Bot. Calif. 1: 565.
1876 Bentham, George and Wm. Hooker. Gen. Pl. 2: 947.
1878 Gray, Asa. Syn. Fl. N. Am. 2: pt. 1, 275.
1885 Greene, E. L. Bull. Calif. Acad. 1: 96, 210.
1886 Gray, Asa. Syn. Fl. 2: pt. 1: ed. 2, Suppl. 442.
1887 Greene, E. L. Pittonia 1: 36.

1890 Greene, E. L. Pittonia 2: 156.
1891 Wettstein, R. v. Engl. & Prantl, Nat. Pflazenfam. 4^{3b}: 71.
1894 Davy, J. B. Erythea 2: 101.
1895 Brandegee, T. S. Gard. & For. 8: 134, fig. 20, p. 135.
1896 Greene, E. L. Erythea 4: 22.
1905 Abrams, L. R. Bull. Torr. Bot. Club. 32: 540–41.
1906 Eastwood, Alice. Bot. Gaz. 41: 287–88.
1924 Grant, Adele L. Ann. Mo. Bot. Gard. 11: 336.
1925 Jepson, W. L. Man. Fl. Pl. Calif. 919.
1935 Munz, P. A. Man. S. Calif. Bot. 477.
1939 McMinn, H. E. Ill. Man. Calif. Shrubs. 498.
1947 Pennell, F. W. Proc. Acad. Phil. Nat. Sci. 99: 168.
1951 McMinn, H. E. Madroño 11: 33–128.

Garden Culture and Horticultural Possibilities

Several attempts to grow *Diplacus* as greenhouse and garden ornamentals have been made since the introduction of seed into England presumably from Menzies' collections in 1792–1794. In fact, the first description of any *Diplacus* was published in 1796 with a colored plate of a garden-grown plant in England from seed collected by Menzies in northern California. Other plants grown in English gardens or greenhouses, without doubt from seed of Menzies' collection, furnished material for the description of at least three named entities by as many authors, but today these are considered to be the same species, namely *Diplacus aurantiacus* (Curt.) Jepson. Subsequent to the early greenhouse culture of *D. aurantiacus,* three other species, *D. grandiflorus, D. puniceus,* and *D. longiflorus,* were grown from seed collected from wild plants in California. Greenhouse-grown plants of *D. grandiflorus,* Azalea-flowered Diplacus, were the sources for three descriptions, presumably of different entities, appearing between 1852 and 1857.

Even though early English plantsmen recognized the ornamental value of this genus, it has not become a popular garden plant in the British Isles because the plants are too tender to thrive there unless grown under glass for most of the year. During the early summer of 1950 I visited many gardens in England, Scotland, and northern Ireland, but I saw only a few plants of *Diplacus* and these were grown in greenhouses. Most of the specimens were identified as *D. aurantiacus, D. puniceus,* or their hybrids and derivatives. In 1937, I observed a few plants, mostly hybrids growing in Devonshire in southwest England where the climate is less severe than in most parts of England.

Sporadic attempts to grow *Diplacus* as garden plants in the United States have met with little success, especially outside of California, and even there I have seen only a few garden collections worthy of note, the better ones being at the Santa Barbara Botanic Garden and at the Rancho Santa Ana Botanic Garden. Only a few nurseries offer for sale any of these entities or their hybrids and derivatives. What are the reasons for this lack of

interest in a group with such an extraordinary range of color in their attractive flowers?

One of the main reasons has been the failure of the plants to survive as perennials under most garden conditions. The fourteen field entities included in this paper, although apparently well adapted to the climatic, edaphic, and biotic conditions in the areas in which they grow naturally, do not thrive when introduced into areas where conditions are dissimilar to those of their native habitats. The adaptability for living in their special geographical and ecological areas has resulted from a strenuous natural selection of those plants possessing the right combination of genes for survival in the particular environments in which each of the wild entities now occurs.

Another reason for the lack of enthusiasm for growing *Diplacus* has been the tendency of the foliage to become brown and dry after flowering, thus giving the plants a ragged and unkempt appearance. The lack of publicity given the numerous color combinations found in some of the more recently improved hybrids, is yet another reason these plants are not more generally cultivated.

Some success in removing these objectionable features has been attained during the six years in which these studies have been in progress. However, much more must be accomplished in improving their adaptability for growing under garden conditions before they can be generally recommended. The two main lines of experimentation have been the hybridization and garden culture of the hybrids, their derivatives, and of the wild entities.

Hybridization. Of the numerous crosses made in the attempt to produce better adapted and more suitable forms for garden use, I shall report upon only a few of the more promising ones. One of the aims of the hybridization work has been to produce a long-lived plant of medium height, with glossy, dark green leaves and numerous large flowers of striking color. In an attempt to produce such a plant (suitable for borders and for bedding plants), *D. grandiflorus,* Azalea-flowered Diplacus, of the northern Sierra Nevada was chosen as one parent because of its typically decumbent habit of growth, glossy, green, glabrous leaves and large, buff-colored flowers with deeply notched corolla-lobes. In its native habitat, this plant is a beautiful subshrub that would be suitable for garden planting without further selection if it were not for its tendency to become straggly and to die within a few years under most garden conditions. *Diplacus rutilus* of southern California was chosen as the other parent because of its vigorous growth, large, dark red flowers and adaptability for living in dry habitats. Although the F_1 progeny did not meet all the requirements set up for our "ideal" plant, they were of sufficiently high quality to warrant giving them a name and recommending them for garden use. They possessed numerous, orange-red flowers

which bloomed over a long period of time, glabrous green foliage, and a growth-form intermediate between that of the two parents. Some of the plants were set out in beds, while others were used as foundation and border plants. Those planted along the foundation of the greenhouse are now four years old, and they continue to bloom profusely and to maintain a healthy and vigorous growth. This cross has been named Grandrutilus (fig. 26) (McMinn, 1949), from a combination of parts of the names of the parents. It can be recommended for planting as a coarse bedding plant, as a filler in informal areas, and for placing in front of medium-height background and screen plantings.

In the hope of reducing the height and improving the foliage, plants of Grandrutilus were backcrossed to both parents. The resulting hybrids showed a most remarkable range in recombination of foliage and floral characters and in form of growth. The flowers were of many hues and intensities of red, copper, buff, and pink. The most striking plants have been chosen for further crossing and selection. Among the second generation plants resulting from "selfing" Grandrutilus, one plant (No. 212-1) had broadly oval, glabrous leaves and exceptionally large somewhat ruffled, and nearly pink flowers with corolla-lobes as deeply notched as those of *D. grandiflorus*. This plant should be a fine addition to our *Diplacus* collection, providing it proves to be adapted to garden conditions.

Another hybrid which has shown potentialities as a good bedding plant resulted from a cross between *D. aridus*, a decumbent plant with glabrous, glossy foliage and light lemon-yellow flowers with reflexed corolla-lobes and *D. rutilus* (see above). This hybrid, known as Blanche McInnes Diplacus (fig. 27) (McMinn, 1949), has tri-colored flowers (red, yellow, and cream-color) with rotate to reflexed corolla-lobes. It has an erect-spreading habit of growth and glabrous, glossy, green foliage. One of the second generation hybrids resulting from this cross resembled the parent *D. aridus* in its decumbent growth-form, foliage characters, and configuration of the corollas, but the flowers were dark red as in the other parent, *D. rutilus*. Its appearance is that of a red-flowered *D. aridus*.

In the Santa Ana Mountains of western Riverside County, there occurs a small hybrid population of *D. longiflorus* × *D. Clevelandii*. Early in the summer of 1945 three of the hybrid plants were marked and in October of that year, Mr. J. H. Munhall collected seed destined for planting in the trial garden at Mills College. From the numerous plants grown from the seeds of lots 17, 18, 19, two were selected for breeding because of their extremely large and deep lemon-yellow flowers. One plant, designated No. 163 (Lot 17-1), was crossed with the red-flowered *D. rutilus*. The flowers of the F_1 hybrids displayed an amazing

range in color, varying from red through different shades of orange, copper, bronze, and pink to white. A few plants had foliage resembling that of *D. Clevelandii,* but most of them had foliage similar to that of *D. longiflorus* and *D. rutilus.* These hybrids and plants grown from their seed give an exceptionally fine display of color during the summer months.

The other plant, designated No. 129 (Lot 19-3), was crossed with *D. grandiflorus* with the hope that its more desirable foliage characters and larger corollas with deeply notched lobes might reappear in some of the progeny. The thirty-five hybrid plants which reached maturity showed various recombinations of characters exemplified by *D. longiflorus, D. Clevelandii,* and *D. grandiflorus.* None, however, had the deeply notched corolla-lobes characteristic of *D. grandiflorus,* but a few had the fine foliage characters of that entity. The overall ornamental effect of these hybrids was so pleasing that they were kept as bedding plants. Many of them, unfortunately died out after one year, a common fate of plants with genes of *D. Clevelandii* when grown in the trial garden.

Plants grown from cuttings and from seed collected from "selfed" plants No. 129 showed a remarkable constancy in the color of their pure lemon-yellow flowers. These plants attracted considerable attention on the part of visitors during the summer of 1949. Inasmuch as their mortality rate is high, new plants should be set out from cuttings made annually.

For those who would like to grow the better selections of *Diplacus,* I recommend the planting of mixed seeds collected from hybrids and the growing of plants made from cuttings of the particular hybrid plant that may strike the fancy.

The following suggestions and recommendations for growing *Diplacus* are based primarily upon my experiences during the past six years in the botanical garden at Mills College. Other growers may have had different experiences and, therefore, would recommend other techniques.

Propagation. *Diplacus* may be propagated by seeds or cuttings. Seeds may be sown anytime during the year, but better germination was obtained with seeds sown in February. The seeds should be sown in flats containing a light sandy loam and covered with about $\frac{1}{8}$ inch of the same type of soil sifted through a very fine-mesh sieve. It is good practice to sprinkle fine sand over the flats to aid in the prevention of damping off of the young seedlings. If the seeds are sown in late fall or during the winter, the flats should be placed in a cold frame or in an unheated greenhouse with rather low humidity. I have had the poorest germination and subsequent highest percentage of damping off of seedlings in flats placed in an artificially heated greenhouse where the humidity was relatively high.

Seedlings normally appear from three to five weeks after the sowing of seed. There have been, however, several instances of

greatly delayed germination. A few seedlings would appear in a flat and when these were about two inches tall, they would be transplanted to other flats or three-inch pots. Two or three weeks later, another crop of seedlings appeared. Evidently certain altered environmental conditions related to the disturbing of the soil were responsible for this second germination. The transplanted seedlings, when about ten inches tall, are ready to plant in their permanent places or in gallon cans if they are to be carried through the summer for late fall planting or through the winter for spring planting.

Since several of the more desirable garden forms of *Diplacus* have resulted from hybridization, it is necessary for their preservation to propagate them by cuttings. Van Rensselaer (1944) reports easy propagation from softwood cuttings, but I have had better results from cuttings made of the older wood. The best results were obtained from heel-cuttings taken from one- and two-year-old growth. As in the case of seed germination, better results have been obtained when the cuttings were grown in an unheated greenhouse. Cuttings have been taken every month of the year from one- two- and three-year-old wood and, although a few have struck from each lot, those taken in the spring as the new growth appears have been the most successful. In a few instances, I have taken ten-inch cuttings from old plants in the field and garden by cutting the stems about six inches from the ground. After most of the lateral branches had been pruned and all but a few leaves removed, the woody stems were placed in gallon cans or in six-inch deep boxes nearly filled with a mixture of about three-fourths coarse sand and one-fourth potting loam. Twenty to fifty per cent of the cuttings struck.

Cultivation. As I have mentioned previously, one of the main objections to *Diplacus* as an ornamental perennial is its high mortality rate under garden conditions. This situation can be alleviated to some extent by proper selection and cultivation. In general, those entities which occur in the wild state close to the garden locality will do better than those growing in other areas. It is important to simulate as nearly as possible in the garden the conditions under which the wild entities grow. This usually involves providing a loose, coarse, often gravelly soil and good drainage. In many cases, the proper selection will necessitate the testing out for one's self of certain wild forms and hybrid entities that have shown vigorous growth and a high survival rate in other gardens. Since the more colorful forms are found in the numerous natural and artificial hybrids, I suggest that these be tried out whenever available. Some of these hybrids have shown exceptional vigor and a low mortality rate. At the Santa Barbara Botanic Garden, hybrids involving *D. longiflorus, D. puniceus, D. aurantiacus,* and *D. rutilus* are reported by Van Rensselaer (1944) to be ten years old and as vigorous and healthy as first-year plants.

In the Mills College garden, hybrids of *D. longiflorus, D. grandiflorus,* and *D. rutilus* have proven quite hardy. In cases of the less hardy but otherwise desirable hybrids, I suggest treating them as annuals. Plants grown from a random collection of seed made annually from garden hybrids will give a fine display of the color variations possessed by the hybrids and will also yield many new recombinations.

Plants set out in late March or April will bloom during late spring and early summer. It is advisable to give them considerable water during the flowering period. If the plants are given a light to medium pruning immediately following their main flowering period, a second period of bloom will occur during the fall months, providing sufficient water is supplied to keep the foliage from drying up. As soon as the second blooming period is over, the plants (if treated as annuals) should be taken out, or (if treated as perennials) cut back to within four inches of the ground. In the climate of the San Francisco Bay area, these plants send out new growth during late February and March, and again produce an abundance of flowers within a few months.

Van Rensselaer (1944) reports that plants of *D. aurantiacus* are grown outdoors successfully on the Atlantic Coast as far north as Washington, D. C., but when grown outdoors farther north, the plants are dug in the autumn and stored in the cellar during the winter. He also reports that *D. aurantiacus* is occasionally cultivated outdoors on the Pacific Coast as far north as British Columbia, and that plants frozen to the ground during the freeze of 1942 recovered and sent up new growth from the base in the spring.

In a cold foggy region it is inadvisable to plant *Diplacus,* as all entities, including the newer hybrids, prefer sunshine and warm temperatures during part of the day.

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